CANADIAN JOURNAL OF RESEARCH

VOLUME 28 DECEMBER, 1950 NUMBER 6

— SECTION D —

ZOOLOGICAL SCIENCES

Contents

Page

Interrelations of Daily Metabolic Cycle, Activity, and Environmental Temperature of Mice—*J. S. Hart* - - - - - 293

Physical and Biological Indicators of the Development of Outbreaks of the Spruce Budworm, *Choristoneura fumiferana* (Clem.) (Lepidoptera: Tortricidae)—*W. G. Wellington, J. J. Fettes, K. B. Turner, and R. M. Belyea* - - - - - - - 308

NATIONAL RESEARCH COUNCIL
OTTAWA, CANADA

CANADIAN JOURNAL OF RESEARCH

The *Canadian Journal of Research* is issued in six sections, as follows:

A. Physical Sciences	D. Zoological Sciences
B. Chemical Sciences	E. Medical Sciences
C. Botanical Sciences	F. Technology

For the present, Sections A, C, D, and E are to be issued six times annually, and Sections B and F, twelve times annually, each under separate cover, with separate pagination.

The *Canadian Journal of Research* is published by the National Research Council of Canada under authority of the Chairman of the Committee of the Privy Council on Scientific and Industrial Research. The *Canadian Journal of Research* is edited by a joint Editorial Board consisting of members of the National Research Council of Canada, the Royal Society of Canada, and the Chemical Institute of Canada.

Sections B and F of the *Canadian Journal of Research* have been chosen by the Chemical Institute of Canada as its medium of publication for scientific papers.

EDITORIAL BOARD

Representing National Research Council	*Representing* Royal Society of Canada	
Dr. H. P. Armes (*Chairman*), Dean of the University, University of Manitoba, Winnipeg, Man.	Dr. G. M. Volkoff, Professor of Physics, University of British Columbia, Vancouver, B.C.	Section III
Dr. Otto Maass, Macdonald Professor of Physical Chemistry, McGill University, Montreal, P.Q.	Dr. J. W. T. Spinks, Dean, College of Graduate Studies, University of Saskatchewan, Saskatoon, Sask.	
Dr. J. H. L. Johnstone, Professor of Physics, Dalhousie University, Halifax, N.S.	Dr. H. S. Jackson, Head, Department of Botany, University of Toronto, Toronto, Ont.	Section V
Dr. A. Bertrand, Professor of Bacteriology, Faculty of Medicine, University of Montreal, Montreal, P.Q.	Dr. E. Horne Craigie, Department of Zoology, University of Toronto, Toronto, Ont.	

Ex officio	*Representing* The Chemical Institute of Canada
Dr. Léo Marion, Editor-in-Chief, Division of Chemistry, National Research Laboratories, Ottawa, Ont.	Dr. H. G. Thode, Department of Chemistry, McMaster University, Hamilton, Ont.
Dr. H. H. Saunderson, Director, Division of Information Services, National Research Council, Ottawa, Ont.	

EDITORIAL COMMITTEE

Editor-in-Chief,	Dr. Léo Marion	Editor, Section D,	Dr. E. Horne Craigie
Editor, Section A,	Dr. G. M. Volkoff	Editor, Section E,	Dr. J. B. Collip
Editor, Section C,	Dr. J. W. T. Spinks Dr. H. G. Thode	Editor, Section F,	Dr. J. A. Anderson Dr. G. M. Volkoff Dr. H. G. Thode
Editor, Section C,	Dr. H. S. Jackson		

Manuscripts should be addressed:

Editor-in-Chief,
Canadian Journal of Research,
National Research Council, Ottawa, Canada

NOTICE

The Canadian Journal of Research is at present published in six sections, A to F. Starting with January 1, 1951, these sections will be published as separate journals under distinctive names and the designation Canadian Journal of Research will no longer be used. The present names and the corresponding new names are as follows:

Present Name	New Name
Canadian Journal of Research, Section A (Physical Sciences)	Canadian Journal of Physics
Canadian Journal of Research, Section B (Chemical Sciences)	Canadian Journal of Chemistry
Canadian Journal of Research, Section C (Botanical Sciences)	Canadian Journal of Botany
Canadian Journal of Research, Section D (Zoological Sciences)	Canadian Journal of Zoology
Canadian Journal of Research, Section E (Medical Sciences)	Canadian Journal of Medical Sciences
Canadian Journal of Research, Section F (Technological Sciences)	Canadian Journal of Technology

In order to preserve continuity the present sequence of volume numbers will be retained, and in each case the volume for 1951 will be Volume 29.

The subscription rates for the Journals will remain as at present.

Canadian Journal of Research

Issued by THE NATIONAL RESEARCH COUNCIL OF CANADA

VOL. 28, SEC. D. DECEMBER, 1950 NUMBER 6

INTERRELATIONS OF DAILY METABOLIC CYCLE, ACTIVITY, AND ENVIRONMENTAL TEMPERATURE OF MICE[1]

BY J. S. HART[2]

Abstract

The daily metabolic cycle of fully fed, adult white mice, at temperatures from −8° C. to 37° C., averaged 48 ml. of oxygen per mouse per hour between the highest nocturnal and lowest diurnal values, but this value was significantly greater at the higher temperatures. Over the same temperature range, forced activity of mice in a rotating metabolism chamber, up to approximately one-half the maximum running speeds studied, resulted in direct superimposition of work metabolism upon that of rest, with a constant metabolic increment at all temperatures. At the maximum running speeds the metabolism produced by the work decreased with decreasing temperature, with some gain in efficiency. The daily metabolic cycle fell within the activity range in which a given degree of work produced the same increment in oxygen consumption at all temperatures. These studies lead to the hypothesis that, in mice, some of the metabolic components of the daily cycle are additive over the biokinetic range. This results in a very large energy expenditure at low temperatures.

Introduction

The energy expended to maintain the same body heat content in homoiotherms must increase when a decrease in environmental temperature occasions an increase in heat loss. In addition, they must expend energy for activities such as obtaining food and escaping from enemies (economic maintenance). There are three hypotheses (13, 14) concerning the interaction of the energy expended for thermoregulation and that expended for activity: the heat production by activity may be added directly to that required for maintaining body temperature at rest (addition hypothesis), the heat production by activity may replace that produced during rest (total substitution hypothesis), the heat production by activity may be added to that produced during rest at warm temperatures and may partially replace that produced during rest at cold temperatures (partial substitution hypothesis). The last concept is embodied in Rubner's "compensation theory" (23).

The partial substitution hypothesis demonstrated for humans (15; 16; 18, p. 420) has been generally assumed to apply for all homoiotherms. However, indications of a departure from the findings for humans have been obtained

[1] *Manuscript received in original form March 28, 1950, and, as revised, June 27, 1950. Contribution from the Division of Applied Biology, National Research Laboratories, Ottawa, N. R. C. No. 2213.*

[2] *Physiologist.*

[The October issue of Section D (Can. J. Research, D, 28 : 249-291. 1950) was issued October 23, 1950.]

for white mice (3) for which the metabolism during work was greater at 21° C. than at 29° C., and the additional oxygen consumed for the work was similar at both temperatures. Contrary evidence arose from a study at 10° C. (19) which indicated that the oxygen consumption was the same in mice during work and rest.

The effect of environmental temperature on metabolism during activity has a bearing on the effect of temperature on the daily metabolic cycle. This cycle is a prominent feature in many mammals and in white mice, which are nocturnal, the peak oxygen uptake may be more than double the minimum during the day (20, 22). If the additional metabolism of activity in mice is added to resting metabolism at warm temperatures, but replaces a portion of the resting metabolism at lower temperatures, then for the same degree of activity there should be a diminution in the magnitude of the metabolic cycle as the temperature is lowered. Again, specific information on mice is meager. However, evidence obtained on pigeons (2, 5) indicated little effect of temperature on the amplitude of the cycle.

Since the available information was limited, work was begun to study the effect of temperature on the daily metabolic cycle and on the metabolism of white mice at various work levels.

Methods

The oxygen consumption of white mice was determined during rest and work at seven temperature levels from −9.6° to 37° C. During rest, measurements were made on four mice simultaneously, from the morning of one day until the morning of the next. This period comprised about 22 out of the 24 hr. in which time the characteristics of the metabolic cycle could be observed. During activity, the oxygen consumption of single mice running in a treadmill was measured at rest and at three work levels, designated as light, moderate, and maximum exercise. All activity measurements were made during the day, and the time for a complete test, including the three work levels, did not exceed three hours.

Daily Cycle of Metabolism in Resting Mice

In each experiment four mice were used in individual respiration chambers. These chambers were brass cylinders, 8.3 cm. in diameter and 18.5 cm. long, painted dull black on the inside. During the tests they were placed vertically, side by side. Each chamber was closed at the top by a No. 12 rubber stopper which contained three tubes, one for the air inlet, one for the air outlet, and one for a tube conveying drinking water. The stopper also contained a glass observation window, 5.0 cm. in diameter. Each mouse was suspended in a cylindrical wire cage, 7.0 c.m. in diameter and 12.7 cm. long, which was fastened to the stopper. The latter was dipped in rubber latex to reduce conductive heat loss from the animal. The urine and feces fell through the cage into paraffin oil at the bottom of the chamber.

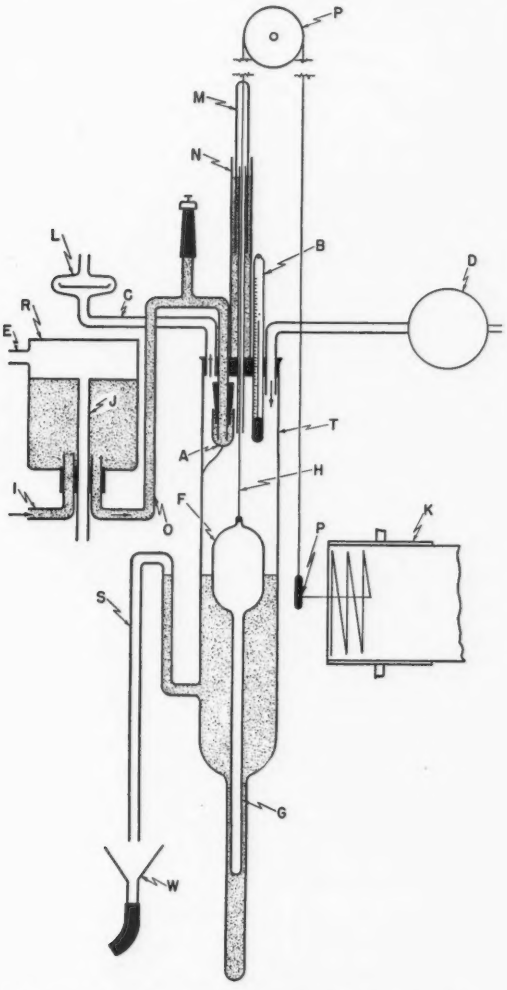

FIG. 1. *Automatic burette and recording apparatus*

A. Water inlet from reservoir with thread to prevent splashing
B. Thermometer
C. Oxygen outlet to respiration chambers
D. Oxygen demand valve
E. Emergency overflow
F. Glass float attached to thread H which moves recording pen P
G. Glass plunger of float
H. Nylon thread
I. Water inlet to reservoir
J. Overflow tube from reservoir
K. Kymograph
L. Check valve
M–N. Water to air seal
O. Water outlet with bubble trap
P. Pulley and recording pen
R. Water reservoir
S. Siphon tube
T. Burette tube
W. Funnel for exhaust water

A closed system was used in which the air was circulated at approximately 500 ml. per minute per mouse by pumps, one for each chamber, and returned to the mice free of water vapor and carbon dioxide. The exhaust air entered a common system in which water vapor was absorbed by magnesium perchlorate and carbon dioxide was absorbed by "Ascarite". The carbon dioxide absorbers were contained within canisters and were removed periodically and weighed to determine carbon dioxide production. Oxygen was added automatically to the circuit between the carbon dioxide absorbers and the pumps. The whole system was submerged in a water bath to control the temperature and, incidentally, to detect leaks.

At temperatures below freezing, water in the bath was replaced with alcohol, the drinking tube was removed, and the exhaust air was dried by a small drying tube placed within the chamber.

The apparatus for supplying and recording the oxygen consumed (Fig. 1) was an automatic siphon burette and demand valve system which differed in a number of features from an automatic system previously described (17). Unlike the previous method, the present system possessed no mechanism for presaturating the water in the burette with oxygen, and the room and water temperatures were not controlled. Corrections were applied for the small errors introduced by these omissions. The oxygen consumption was recorded mechanically and no electric devices were used. When oxygen is consumed by the animals, the pressure in the burette falls and water flows from the reservoir R at a rate equal to the rate at which oxygen is consumed. This flow of water raises the water level in the burette and the latter operates the recording system.* During this phase of the cycle no oxygen flows from the demand valve because the pressure in the burette is slightly above that of the atmosphere. When the water level reaches the bend in tube S, the siphon empties the system and oxygen is drawn in to replace the water. During this phase of the cycle the pressure in the burette is below that of the atmosphere and oxygen is drawn from the valve faster than water can be supplied from A. The siphon "breaks" when the water level falls below the inlet of tube S, and the cycle is then ready to repeat.

A record obtained on the kymograph K is shown in Fig. 1. Oxygen recharging produces an almost vertical line. When oxygen is flowing to the animals, a sloping line is produced from which the oxygen consumption is calculated.

Oxygen Consumption of Active Mice

The apparatus (Fig. 2) for measuring oxygen consumption during activity is similar to those previously described (1, 3). It consists of a movable treadmill enclosed by a stationary metabolism chamber which can be submerged in a water or alcohol bath. The cage containing the mouse is fitted with a baffle that hangs vertically from the shaft of the apparatus. This baffle is necessary to keep the mouse running but if the rotation speed is too fast the baffle also rotates and the mouse is then able to ride the cage.

* *The stroke of the system was 14 cm. and the volume 17.0 ml. per cm.*

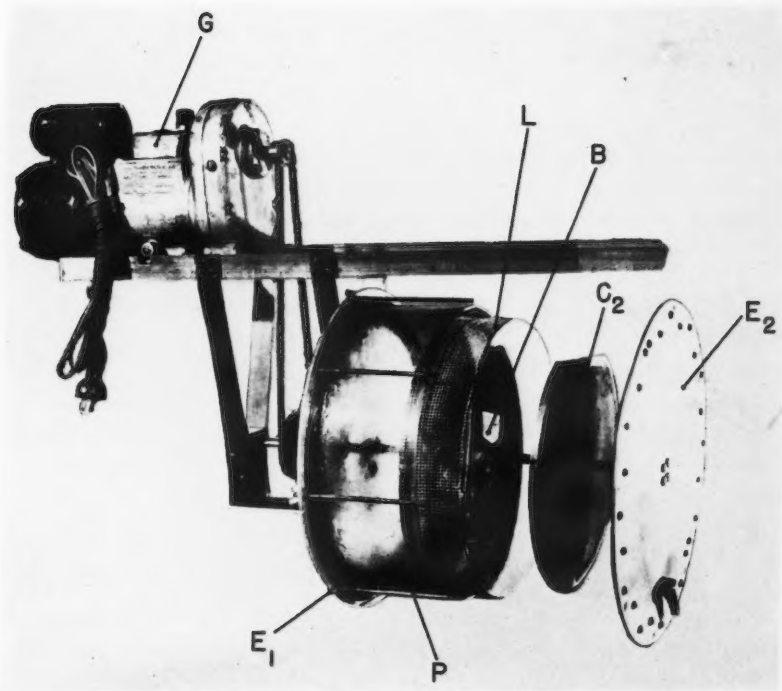

FIG. 2. *Metabolism chamber with treadmill.*

B. *Baffle to stimulate running of mouse*

C_2. *Canister fitting loosely on shaft on each side of treadmill, containing carbon dioxide and water absorbent*

E_1. *Fixed metal plate*

E_2. *Removable plate containing a circular slot 0.125 in. wide to fit plastic cylinder. "Duxseal" (Johns-Manville Corp.) used in slot for air to water seal. Oxygen inlet tube shown on plate.*

Carbon dioxide was absorbed within the chamber and oxygen consumption was measured in a manner similar to that described for resting mice except that a 250 ml. dispensing burette replaced the automatic burette. Here, readings of the water replacement of the oxygen consumed were made directly.

Temperature Control

Temperatures were measured by thermocouples placed on the walls of the respiration chambers and also placed in the air near the exhaust tubes of the "rest" metabolism chambers, and near the oxygen inlet below the cage of the "activity" metabolism apparatus. Air temperatures fluctuated within $\pm$ 0.3° C. in the chambers. The mean of air and wall temperatures was taken as the environmental temperature (Tables I and III).

History of Mice

For three weeks prior to the tests and when actually not under test the mice were kept in a room at approximately 6° C. in cages containing wood shavings. During this period the light was kept at a low level and controlled by a time switch with an "on" period from 6 A.M. to 6 P.M. The animals were fed ad libitum on a mixed diet containing 16% fat and 20% protein. Food was also supplied in the form of pellets during the tests on resting metabolism.

Body Weights

Throughout the experimental period, the average body weight was 26.72 gm., the average gain in weight was 0.8 gm. and the maximum gain was 1.4 gm. However, on the average, weight was lost during actual tests. The maximum weight loss per day, in rest experiments, at −8° C., averaged 4.4 gm. At 32.2° C., the losses ranged between 1.0 and 3.0 gm. per day. In all other rest experiments the average was 0.3 gm. per day. During activity the weight loss averaged 2.0 gm. per mouse at −9.6° to 32.0° C., but at 37.0° C., the loss was 2.6 gm. per mouse.

Experimental Procedure

A total of 10 males and 10 females, in five groups of four, at an initial age of six to eight weeks were used in a series of experiments that lasted 17 weeks. The series was carried out in two steps. In the first, 12 mice were tested at each of five temperatures between 2° and 32° C. during the daily metabolic cycle tests at rest and during activity; in the second, eight mice were tested at −8.0° to −9.6° C. and at 37° C. during the cycle tests at rest and during activity. The order of the experiments respecting temperatures and individuals was randomized to eliminate any effects of advancing age. One mouse died at the beginning of the first series and this was replaced by a mouse of the same stock and similar age. Eight mice died in the second series at 37° C. and four at −8° C.

At the start of a 20 to 22 hr. rest experiment, four mice were introduced into the chambers at approximately 10 A.M. and the record was started about an hour after temperature equilibrium had been established. These experiments were left undisturbed until the next morning unless carbon dioxide

production was also being measured, in which event absorption bottles were changed at six to eight hour intervals. A dim light was left on during the night to facilitate the changing.

At the start of a two to three hour activity experiment, a mouse was introduced into the chamber during the morning or afternoon and determinations started about an hour after temperature equilibrium had been extablished. The procedure involved the following: first, measurement of oxygen consumption when the cage was not in rotation; secondly, measurement of oxygen consumption at a running speed of 4.25 per sec., with two to four separate 10-min. readings: this was designated "light exercise"; thirdly, measurement of oxygen consumption at a running speed of 9.9 cm. per sec., with two to four separate 10-min. readings: this was designated "moderate exercise"; and finally, similar measurements at the maximum running speed. There were no rest periods in these tests, but about 5–10 minutes was required between changes of activity levels for carbon dioxide production and oxygen consumption to reach steady values. The separate readings for each activity level were averaged.

The maximum running speed was variable. The cage speed was increased gradually until the mouse began to "ride" the cage, and then the speed was reduced until he kept his customary position at the bottom or towards the front of the cage. When the animals have been running for relatively long periods of time, this maximum pace should correspond to a state at which oxygen debt is not steadily accumulating or is accumulating very slowly. The point at which a mouse passed from running to riding was not very precise, particularly at 37° C. when they would sometimes run to exhaustion without riding the cage. However, the average value of this maximum rate appears to be useful for determining an upper voluntary limit for work and energy production at different temperatures. The use of the term "voluntary" here signifies the maximum to which the mice can be made to run under the conditions of the experiment; it is not necessarily the maximum steady effort of which the mice are capable.

Results

Maximum Running Speeds

The average values for the maximum running speeds are shown in Table I. The white mice could not be encouraged to run very fast in these tests. The highest maximum value (at 18° C.) was below 20.3 cm. per sec. (40 ft. per min.).

Temperature had little effect on the maximum running speed between 2° and 32° C. but it fell off above and below this range. At −9.6° C. only three mice ran at the 9.9 cm. per sec. level, a speed designated as moderate exercise, and the average maximum rate was 8.5 cm. per sec. At 37° C. the mice behaved in an erratic fashion. One mouse would not run faster than about 4 cm. per sec., while three died after running at speeds exceeding 13 cm. per sec. Consequently, to avoid lethal effects, the mice were not exercised at speeds exceeding the 10 cm. per sec. level. This work level seemed to be the

TABLE I

DIFFERENCE IN AVERAGE "WORK" AND "REST" OXYGEN CONSUMPTION VALUES (OXYGEN INCREMENT OF WORK) AT DIFFERENT TEMPERATURES AND RUNNING SPEEDS

Mean of wall and air temp. during work, °C.	Diff. in mean temp. during work and rest, °C.	Oxygen increment of work, ml. per mouse per hour, S.T.P.			Max. running speed, cm. per sec.
		Light work, 4.25 cm. per sec.	Moderate work, 9.9 cm. per sec.	Maximum work	
−9.6	1.6	65 (8)*	74 (3)	54 (8)	8.5
2.1	1.3	52 (13)	61 (12)	75 (12)	18.0
10.0	0.8	59 (12)	78 (12)	98 (12)	18.5
18.0	0.6	60 (12)	82 (12)	116 (12)	19.5
26.0	0.4	54 (12)	76 (12)	113 (12)	17.8
32.0	0.2	57 (12)	80 (12)	118 (12)	16.5
Average		57 ± 4	75 ± 4		

* *Figures in brackets are the numbers of individuals in work tests.*

maximum compatible with nonlethal effects in activity tests, but it was apparent that the mice were capable of higher speeds at this temperature.

Daily Cycle of Metabolism of Resting Mice

The average oxygen uptake for consecutive one to two hour periods from 12 noon approximately until about 10 a.m. was determined for groups of four mice at temperatures from −8.0° to 32.2° C. The oxygen uptake at 37° C. could not be determined over the same time period because the mice died after an exposure of three hours or more at this temperature. Determinations during the first few hours of such tests were, however, used for comparison with activity data (Fig. 5). Respiratory quotients were also estimated for some of the tests (Table II). They were quite variable and no trend was noted with temperature or period of day.

TABLE II

RESPIRATORY QUOTIENTS IN RELATION TO TEMPERATURE AND PERIOD OF DAY

(Each column represents one experiment)

Approximate period	Temperature, °C.							
	−8.0	3.4	10.8		18.6	26.4	32.2	
11 A.M. – 7 P.M.	0.88	0.84	0.91	0.79	0.80	0.90	0.93	0.82
7 P.M. – 2 A.M.	.85	.80	.90	.84	.82	.88	.94	.86
2 A.M. – 9 A.M.	.81	.88	.91	.80	.84	.92	.93	.95
Mean	.86	.84	.91	.81	.82	.90	.93	.88

Details of the variation in metabolic rate with time of day are shown for two temperatures in Fig. 3. There was considerable variation in the records but at each temperature there was a maximum uptake during the night and

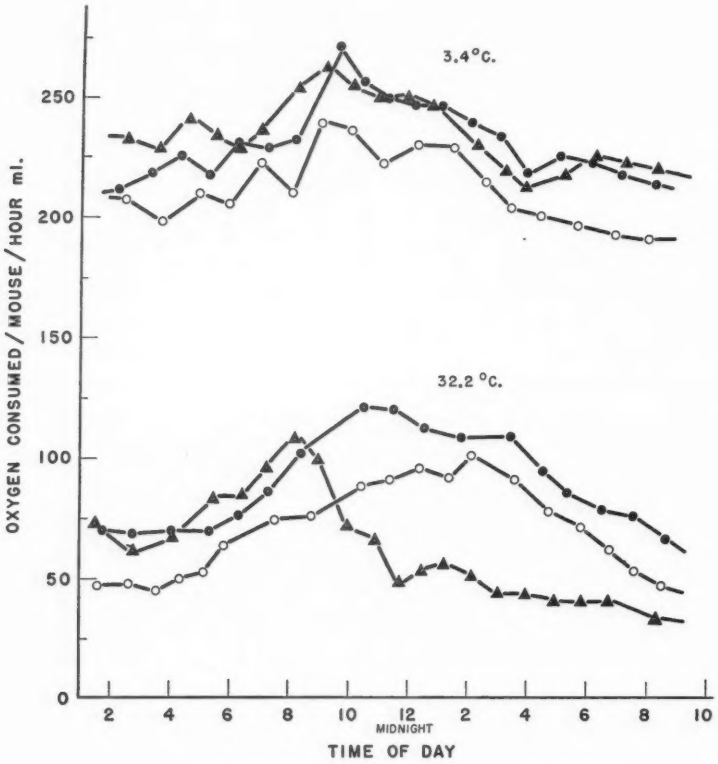

FIG. 3. *Daily metabolic cycle at different temperatures.*

a minimum during the day. The variation in times of occurrence between groups of the maximum and minimum values, summarized in Table III, was greatest at 32.2° C. for maximum and at 26.4° C. for minimum values.

Since the maxima and minima did not occur at the same time in different groups at the same temperature, or even in the same groups at different temperatures, it is to be expected that the variation would be even greater had single mice been studied. These phase differences in the cycles of the mice would render the observed amplitudes of the cycles less than the true amplitudes for single animals. However from the viewpoint of the writer the important feature of the cycles was that they persisted at all temperatures and did not disappear in the cold.

TABLE III

TIMES OF OCCURRENCE OF HIGHEST AND LOWEST VALUES OF DAILY METABOLIC CYCLE AT DIFFERENT TEMPERATURES

Mean temperatures, °C.				Time of highest value	Time of lowest value
Bath	Wall	Air	Mean of wall and air		
−9.8	−9.3	−6.8	−8.0	9.00 P.M.	5.00 A.M.
2.0	2.4	4.4	3.4	9.30 P.M. 9.30 P.M. 9.00 P.M.	8.00 A.M. 8.15 A.M. 4.00 A.M.
10.0	10.2	11.3	10.8	11.00 P.M. 1.30 A.M. 11.30 P.M.	9.00 A.M. 8.30 A.M. 8.30 A.M.
18.0	18.1	19.1	18.6	12.00 A.M. 11.30 P.M. 10.30 P.M.	8.00 A.M. 7.15 A.M. 8.00 A.M.
26.0	26.0	26.7	26.4	1.00 A.M. 1.15 A.M. 10.40 P.M.	8.45 A.M. 8.20 A.M. 4.00 A.M.
32.0	32.0	32.4	32.2	2.00 A.M. 8.00 P.M. 11.00 P.M.	8.30 A.M. 8.15 A.M. 8.40 A.M.

The highest and lowest values of the metabolic cycle have been plotted against temperature in Fig. 4 and suggest on inspection that the amplitude of the cycle was greater at the higher temperatures studied. These data were subjected to statistical analysis:—

There were data for one group of mice at −8.0° C. and for three groups at each of +3.4°, 10.8°, 18.6°, 26.4°, and 32.2° C. These provided 10 degrees of freedom for a combined estimate of the intergroup, intratemperature standard deviation of recorded amplitudes, which was found to be ±8.9 ml. per mouse per hour, some 18% of the mean amplitude of 48.1 ml. An analysis of variance (6) in which the intertemperature sum of squares was divided into a portion corresponding to one degree of freedom associated with the regression of amplitude on temperature and another portion, corresponding to four degrees of freedom associated with deviations from this regression, gave, when the resulting mean squares were compared with the foregoing intergroup intratemperature variance, $F = 7.69$ and $F = 1.55$ respectively. The chance probability of the former was about .025 and that of the latter was about .25 from which it may be concluded that the amplitude of the daily metabolic cycle was significantly affected by temperature. It is possible that this effect was in fact confined to the two highest temperatures, but this cannot be asserted from the data.

The cause of the increase in amplitude of the cycle with temperature can only be surmised at present. It may be associated with a greater amount of activity or with a higher oxygen uptake due to feeding with increase in temperature. The latter was found for rats by Swift (24). It will be shown that there is no evidence that the increase is due to partial replacement of resting thermogenesis by metabolism of activity at the lower temperatures.

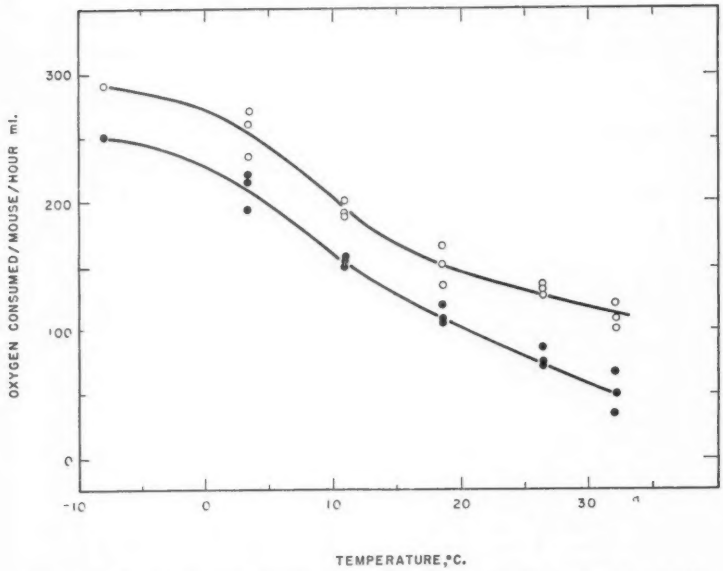

FIG. 4. *Minimal* (●) *and maximal* (○) *oxygen consumption in daily metabolic cycle in relation to temperature for each group of four mice.*

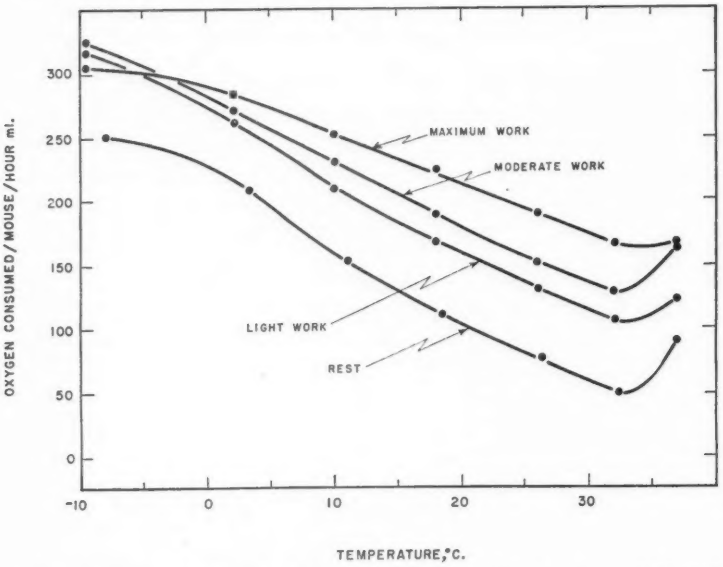

FIG. 5. *Effect of temperature upon oxygen consumption during rest, light work (speed 4.25 cm. per sec.), moderate work (speed 9.9 cm. per sec.), and maximum work. Data for rest are average of lowest values in daily cycle except at 37° C. where they are average of lowest values in tests lasting three to five hours.*

Oxygen Consumption During Activity at Different Temperatures

The average oxygen consumptions during rest (lowest observed values), light work (4.25 cm. per sec.), moderate work (9.9 cm. per sec.), and maximum work are illustrated in Fig. 5, while the temperature conditions of the experiments, the difference between average resting and working values (oxygen increment of work) and running speeds are given in Table I. The data for oxygen consumption during rest are the minima of the daily cycle from $-8.0°$ to 32.2° C. but at 37° C. they are the lowest values obtained in the first few hours at this temperature (see section on metabolism of resting mice). Tests were carried out to determine whether temperature affected the oxygen increments produced by light and moderate work which were constant levels at different temperatures, and maximum work which was not entirely constant at different temperatures.

The oxygen increments listed for three exercise levels at the same temperature are not statistically independent, partly because all involve the same determinations of oxygen consumption at rest, and partly because of some actual correlation in the oxygen consumption for the same mouse throughout any one period in the metabolism apparatus. Since this correlation (specified by an intraclass correlation coefficient of $r = 0.5$) did not extend to measurements made with the same animal on different occasions, analysis of covariance procedure was again used to test the statistical significance of any recorded variation in the average oxygen increment of work with temperature. Single measurements of oxygen consumption at the same temperature and work level varied considerably, with a standard deviation of ± 23 ml. per mouse per hour. The ratio of the intertemperature to the intratemperature variance of the oxygen increment of light work was $F = 0.3$, $P = .9$ approximately. For moderate work the ratio was $F = 0.6$, $P = .7$ approximately, while for maximum work it was $F = 5.2$, $P < .01$. Division of the intertemperature variance of the oxygen increment of moderate work into a component with one degree of freedom due to any linear regression of oxygen increment of work on temperature and a second component with four degrees of freedom due to the recorded intertemperature variance not thus accounted for gave $F = 1.2$, $P = .3$ approximately for the former and $F = 0.5$, $P = .7$ approximately for the latter when the resulting mean squares were tested against the intratemperature variance. Corresponding calculations for the oxygen increment of maximum exercise gave $F = 22.6$, $P < .001$, and $F = 0.8$, $P = .5$ approximately for the two components. A further analysis of covariance was not indicative of any appreciable effect on the recorded oxygen increments of the differences, ranging up to 1.6° C., noted in the mean temperature within the rest and activity metabolism apparatus.

It has been concluded from the foregoing analyses that the experimental results did not demonstrate any significant change in the oxygen increment of light work with temperature, and that the results for moderate work could likewise hardly be regarded as definitely suggesting such an effect, which however was clearly evident in those for maximum work. The recorded average increments listed in Table I suggest on inspection that this last effect was possibly confined to the lower two-thirds of the temperature range. However, the foregoing analysis of variance indicated that in relation to the intratemperature variance of individual observations the evidence for this was not strong, and the most to be inferred statistically was that the trend with temperature was, on the whole, upwards to an extent approximately specified by a regression coefficient of 15 ± 3 ml. per mouse per hour per 10 Centigrade degrees.

The study of oxygen consumption of white mice during rest and work has shown, in general, that both temperature and work produced additive effects on metabolism. At speeds below about one-half the maximum level, the same amount of work was done with approximately the same increase in oxygen consumption at all temperatures. The tendency towards maximum energy expenditure at low temperatures is indicated by a greater oxygen uptake during the rest at −8.0° C. than during maximum work at 32° C. The highest oxygen uptake, which occurred at −9.6° C. during work was 325 ml. per mouse per hour. This value is about 7.6 times the basal rate (per gram) reported by Morrison (21) and is 6.5 times the lowest rate found in the present study. Even at maximum work, the mice used considerably more oxygen at low than at high temperatures. The gross efficiency of the work therefore decreased as the temperature decreased. These data suggest that the maximum attainable energy turnover of mice is not the same at different temperatures, as was suggested by Kendeigh (12) for birds, but is greater at low than at high temperatures.

The data obtained at 32.2° and 37° C. during rest and work, although complicated by lethal effects at the latter temperature, further suggest (Fig. 5) that the oxygen increment of work was added directly to that found during rest. During both rest and work there was an increase in oxygen consumption with increase in temperature from 32.2° to 37° C. which was probably caused by hyperthermal rise associated with suppressed heat loss. There was also no evidence from these data that the thermal zone of minimum metabolism, in the neighborhood of 32° C., underwent a shift to lower temperatures during activity.

Discussion

A finding of major interest in this investigation is that a given amount of work produced the same increase in oxygen consumption at all temperatures when the work level, in terms of running speed, was below about one-half the maximum rate. This evidence for the addition hypothesis is in agreement with the observations of Chevillard (3), who found approximately the same oxygen increment of work at 21° and 29° C. in mice, but differs from the observations of Magne (19) who found that, at 10° C., heavy work did not increase the oxygen consumption of mice above the resting level at this temperature.

It is premature to attempt an explanation, from the available evidence, of the apparent discrepancy between these results and those of Lefévre and others which indicate that homoiotherms economize on energy at low temperatures by "using" the heat produced by muscular activity as a substitute for some or all of that required to maintain body temperature during rest. In this study nothing is known concerning the partition of heat loss by radiation, convection, and particularly by evaporation during rest and work at different temperatures, and further study of these factors is essential for an understanding of the phenomena observed. Suffice it to say that the application of the partial

substitution hypothesis even for humans is not so widely applicable as might be inferred from the older literature, since data obtained by Horvath *et al.* (11) indicated that metabolism for a standard grade of work showed a greater increase over resting values at −29° C. than it did at 25° C.

In the interpretation of the decreasing oxygen increments of maximum work with decreasing temperature, it must be emphasized that maximum work, although essentially constant in the 2° to 32° C. range, fell off at −9.6°C. and this may have occasioned a reduction in oxygen uptake at this temperature. Nevertheless at these higher working rates there appears to be a reduction in uptake with decreasing temperature that is not accounted for by decreasing working rates. It is therefore possible, although the evidence is inconclusive on this point, that during strenuous work in the cold there is partial replacement of the oxygen consumption of thermogenesis by the oxygen consumption of the work. Another possibility is that thermoregulation within the lower temperature range is breaking down during maximum exercise. Evidence for this hypothesis was obtained by Giaja (8) who found that the oxygen consumption and body temperature of rats showed a marked fall after several hours of exhausting work in the cold.

Since environmental temperature had little effect on the increment of oxygen consumption for light or moderate work in mice, it is easier to understand why the amplitude of the metabolic cycle in resting mice was not greatly reduced at low temperatures. In this study the highest nocturnal values for the daily cycle were below those obtained during light work (4.25 cm. per sec.) at each temperature. In other words the amplitude of this cycle fell entirely within the activity range in which a given degree of work produced the same increment in oxygen consumption at all temperatures. Therefore, the same degree of voluntary activity of mice that are not restricted in any way should produce the same metabolic increment during the daily cycle at all temperatures.

The failure of the nocturnal increment in oxygen consumption to be greatly lessened or to disappear at low temperatures in these mice agrees in general with the findings for pigeons (2, 5), and it is possible that this phenomenon is general in small homoiotherms. The cause of the increase in the magnitude of the cycle at the higher temperatures in this study is not known but it may be associated with differences in the degree of voluntary activity present at different temperatures, or with variations in the heat increment of feeding. In support of the latter, the work of Swift (24) showed that the increase in oxygen consumption due to feeding in rats was greater at warm temperatures than at cold temperatures.

Since the effect of environmental temperature is similar on both the amplitude of the daily metabolic cycle and on the oxygen increment of activity, and since cyclic variations in metabolism coincide with activity variations measured mechanically (9) or estimated by observation (4, 7, 10), it is evident that voluntary activity plays a large part in the metabolic cycle. Eventually, it may be possible to estimate the energy utilized by this voluntary activity

by analysis of the metabolic cycle, if the energy utilized by other contributing factors, such as heat increment of feeding, can also be estimated. Investigations are being continued on this problem.

Acknowledgments

The writer wishes to acknowledge the technical assistance of Mr. L. Blevis and to thank Dr. J. W. Hopkins for statistical appraisal of the data. He is also indebted to Dr. F. E. J. Fry for helpful suggestions in the preparation of the manuscript.

References

1. ASHER, L. and CURTIS, G. M. Beiträge zur Physiologie der Drüsen. Untersuchungen über den respiratorischen Stoffwechsel bei Arbeit in seiner Beziehung zu den Drüsen mit innerer Secretion. Biochem. Z. 164 : 97-109.
2. BURCKARD, E., DONTCHEFF, L., and KAYSER, Ch. Le rythme nycthéméral chez le pigeon. Ann. physiol. physicochim. biol. 9 : 303-368. 1933.
3. CHEVILLARD, L. Contributions à l'étude des échanges respiratoires de la souris blanche adulte. II. Thermogénèse et thermolyse de la souris. Ann. physiol. physicochim. biol. 11 : 485-532. 1935.
4. DEIGHTON, T. and HUTCHINSON, J. C. D. Studies on the metabolism of fowls. II. The effect of activity on metabolism. J. Nutrition, 30 : 141-157. 1940.
5. DONTCHEFF, L., KAYSER, CH., and REISS, P. Le rythme nycthéméral de la production de chaleur chez le pigeon et ses rapports avec l'excitabilité des centres thermorégulateurs. Ann. physiol. physicochim. biol. 11 : 1185-1208. 1935.
6. FISHER, R. A. Statistical methods for research workers. 10th ed. Oliver and Boyd, Ltd., Edinburgh. 1946.
7. FUHRMAN, G. J., MCLIN, E. D., and TURNER, M. L. The effect of time of day on the metabolic rate of albino mice, a manometric method. Am. J. Physiol. 147 : 284-288. 1946.
8. GIAJA, J. Influence de la fatigue musculaire sur la puissance thermogénétique et la résistance au froid. Ann. physiol. physicochim. biol. 8 : 535-545. 1932.
9. HERRING, V. V. and Brody, S. Diurnal metabolic and activity rhythms. Univ. Missouri Agr. Coll. Research Bull. No. 274. 1938.
10. HORST, K., MENDEL, L. B., and BENEDICT, F. G. The effects of external factors upon the metabolism of the rat. J. Nutrition, 7 : 277-303. 1934.
11. HORVATH, S. M., FREEDMAN, A., and GOLDEN, H. Acclimatization to extreme cold. Am. J. Physiol. 150 : 99-108. 1947.
12. KENDEIGH, S. C. Effect of temperature and season on energy resources of the English sparrow. Auk, 66 : 113-127. 1949.
13. LEFÉVRE, J. Chaleur animale et bioénergétique. Masson et Cie, Paris. 1911.
14. LEFÉVRE, J. and AUGUET, A. Le problème des relations entre les chaleurs du travail et du repos. Pourquoi le travail est plus économique aux basses températures. Compt. rend. 192 : 819-820. 1931.
15. LEFÉVRE, J. and AUGUET, A. La thermorégulation du travail. Rapports de ses courbes avec celles du repos. Ann. physiol. physicochim. biol. 9 : 1103-1121. 1933.
16. LEFÉVRE, J. and AUGUET, A. Les courbes thermorégulatrices et les rendements de la machine vivante dans les grandes puissances de travail. Ann. physiol. physicochim. biol. 1116-1134. 1934.
17. LEWIS, H. G. and LUCK, J. M. An apparatus for automatically measuring the respiratory exchange of small mammals. J. Biol. Chem. 103 : 204-226. 1933.
18. LUSK, G. The elements of the science of nutrition. 4th ed. W. B. Saunders Co., Philadelphia & London. 1931.
19. MAGNE, H. Influence de la température extérieure, sur la grandeur de la dépense d'énergie occasionnée par le travail musculaire. Comp. rend. soc. biol. 83 : 396. 1920.

20. MORRISON, P. R. Oxygen consumption in several small wild animals. J. Cellular Comp. Physiol. 31 : 69-96. 1948.

21. MORRISON, P. R. Oxygen consumption in several mammals under basal conditions. J. Cellular Comp. Physiol. 31 : 281-291. 1948.

22. PEARSON, O. P. The rate of metabolism of some small mammals. Ecology, 28 : 127-145. 1947.

23. RUBNER, M. Die Gesetze des Energieverbrauches bei der Ernährung. F. Dieticke Co., Leipzig and Vienna. 1902.

24. SWIFT, R. W. The effect of feed on the critical temperature of the albino rat. J. Nutrition, 28 : 359-364. 1944.

PHYSICAL AND BIOLOGICAL INDICATORS OF THE DEVELOPMENT OF OUTBREAKS OF THE SPRUCE BUDWORM, *CHORISTONEURA FUMIFERANA* (CLEM.) (LEPIDOPTERA: TORTRICIDAE)[1]

By W. G. Wellington,[2] J. J. Fettes,[2] K. B. Turner,[3] and R. M. Belyea[2]

Abstract

Biological and meteorological records were examined for periods when outbreaks of the spruce budworm, *Choristoneura fumiferana* (Clem.), were known to have occurred in northeastern North America. The survey showed that the following significant events occurred during the period of three to four years preceding an outbreak. Decreasing annual numbers of low pressure centers passed over the area in which the outbreak later occurred. Therefore, the outbreak began at a time of decreased or minimal storminess. Drought occurred, chiefly in June and July, but also occasionally in spring and autumn. Annual increments of host trees on dry sites declined. Outbreaks of the forest tent caterpillar, *Malacosoma disstria* Hbn., occurred, particularly in Ontario. These events, in aggregate, occurred so consistently before spruce budworm outbreaks that they have future predictive value. In addition, they reinforce some suggestions made by earlier authors and suggest modifications of hypotheses concerning the behavior of developing populations of the spruce budworm.

Introduction

The spruce budworm, *Choristoneura fumiferana* (Clem.), is an insect of major economic importance in the forests of eastern North America, notably in those of the Canadian provinces of New Brunswick, Quebec, and Ontario. Two earlier infestations, beginning about 1909 and 1913, were studied by Swaine *et al.* (28). More recent ones, some of which began in 1935 and 1940, brought about the current extensive program of investigations, particularly in Ontario, of which the work reported here has been a part.

No adequate method for the prediction of spruce budworm outbreaks has been available. This implies that some modifications of working hypotheses may be required. Because of the economic status of the insect, any new information suggesting a modification of hypotheses concerning factors controlling its population growth is sufficiently important to warrant serious consideration, even if drawn from circumstantial evidence. This paper describes such information.

Most of the paper is devoted to description of an interesting set of circumstances that have recurred often enough before separate outbreaks in New Brunswick, Quebec, and Ontario to preclude coincidence. Sometimes the predictive value of each individual phenomenon has been slight, but, in aggregate in the past, they acted as indicators of approaching outbreaks.

[1] *Manuscript received July 13, 1950.*

Contribution No. 2697, Division of Entomology, Science Service, Department of Agriculture, Ottawa, Canada.

[2] *Forest Insect Laboratory, Sault Ste. Marie, Ont.*

[3] *Division of Timber Management, Ontario Department of Lands and Forests, Toronto, Ont.*

Therefore, as indicators, they could form an integral part of the predictive method essential for any real success in programs designed to minimize the effects of future outbreaks.

The paper has been restricted chiefly to a survey of conditions that appear before outbreaks, but consideration of some of the implications of the recurrence of the indicators has led to the inclusion in the discussion of comments on the outbreak period proper and of comments on some of the current hypotheses.

Materials and Methods

Bioclimatic investigations have been the responsibility of the senior author, following a series of studies on the influence of physical factors upon the insect. The others, in turn, have carried out investigations of population dynamics, forest composition, and tree deterioration, all with special reference to outbreaks of the spruce budworm. Some of the information has been published or is in press, but most of it is still being prepared for publication. Some of these data which are applicable to periods preceding outbreaks have been pooled. Also, information has been made available by colleagues working on closely related projects. In addition, the writers have had access to original maps of the Forest Insect Survey of the Division of Entomology and of earlier workers, which date back to the first decade of this century.

Originally, it was planned to treat each known infestation in the three provinces in sequence, but lack of sufficient background information for many of them made it necessary to restrict the treatment to isolated examples. Information from infestation maps drawn for the Forest Insect Survey has been assessed with regard for the fact that coverage, until recently, has been inadequate. Nevertheless, despite the problems involved in assessing older maps, there is no objection to their use to indicate presence or absence of spruce budworm outbreaks in a region. This has been their sole value for some periods. Some areas received, at all times, better coverage by the Survey than others, and, in each of these, the boundaries or the assigned intensity ratings of an infestation could be accepted with more confidence.

It has been necessary to employ a standard method for selecting the first year of an outbreak, since all investigations of factors related to population growth had to be dated with reference to that year. Earlier workers adopted as the beginning of an outbreak the year in which an unusually wide annual ring was produced in the trees at about breast height. This method meets with some objections, because it is not yet certain what causes such wide rings. Moreover, studies of defoliation have demonstrated that there are three or four years of increase of the insect population prior to the year of formation of the wide ring. Nevertheless, it is precisely these years that are of present concern, so that the datings of earlier workers have been accepted, and similar methods have been used for more recent infestations wherever possible.

Much use has been made of official meteorological data published in the *Monthly Record* of the Meteorological Division, Department of Transport, Canada, and in the *Monthly Weather Review* of the United States Weather Bureau. As with the biological survey data, there were often inadequate records in areas in which earlier infestations occurred. Nevertheless, sufficient examples have been accumulated to reveal definite trends.

The methods of treating meteorological data will become clear in the text. Ordinary statistical techniques have not been applied, for one or the other of components of sets of data provided series too brief to yield to ordinary treatments. Hence, the series can be accepted only as revealing interesting trends rather than actual correlations.

Criticism has been directed at employment of official records in ecological analyses (e.g., 36). Screen temperatures and station precipitation records have often been improperly applied. Yet the same criticism may be directed to ordinary ecological methods of obtaining weather data. Therefore, the controversy is reduced to the following terms: if the action of factors upon an organism have been analyzed sufficiently, and the weather types of a region are sufficiently understood, official records are usually trustworthy tools for the projection of the analytical techniques into otherwise inaccessible areas; otherwise, no type of weather record is to be trusted.

The phenomena observed fall naturally into two broad groups: physical and biological indicators. Before they are considered, it is necessary to outline some pertinent points of spruce budworm ecology.

Physical Requirements of the Spruce Budworm

Throughout earlier literature on the spruce budworm there is an indication that drought is associated with infestations or with the effects of infestations. It was stated (28) that defoliated trees on dry sites succumbed more quickly than other trees. Graham (14) suggested that outbreaks of the spruce budworm may be associated with periods of drought, without elaborating the point. MacAloney (22) included a diagram that showed an extended period of drought before a jack-pine budworm infestation in Minnesota. Franz (13) has shown that amount of defoliation by the closely related European species, *Cacoecia murinana* (Hb.), is associated with the duration of precipitation during the feeding period. Fig. 1 shows an analogous association between the annual amounts of June rainfall at Cameron Falls, Ont., and the percentages of defoliation of a balsam tree at Black Sturgeon Lake, Ont. Details appear in the legend for the figure. (Note: To assist the reader unfamiliar with specific localities referred to throughout the remainder of the text, a base map is shown in Fig. 2.)

Recent investigations (17, 30–35) have shown the effects of light, temperature, and moisture upon spruce budworm behavior and activity. Larvae of the spruce budworm do not feed readily when the air surrounding them in their tunnels is saturated, as it is during steady falls of rain. Solar heating of

buds containing larvae in the early spring enables the insects to move about or feed when air temperatures are low (33, 35). Recently, it has been observed that open winters, with violently fluctuating temperatures in November and

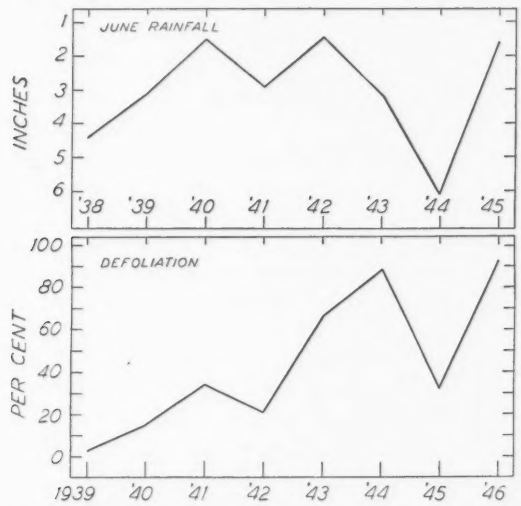

FIG. 1. *Association of the amounts of June rainfall during consecutive years with the percentages of defoliation by the spruce budworm. June rainfall for Cameron Falls, Ont., is plotted with the amounts inverted. Percentage defoliation at Black Sturgeon Lake, Ont., is plotted with a lag of one year.*

December, may be detrimental to larvae overwintering in hibernacula. These facts permit some generalizations on the relation of weather to spruce budworm development.

In the spring, clear or only partly clouded skies during the day provide ideal conditions for development. Dense clouds that obstruct much radiation or produce rain are detrimental. Similarly, throughout the remainder of the feeding period, dry, relatively clear air masses are ideal, and heavy clouds, rain or generally humid air masses are detrimental. During the winter, larvae that have been properly conditioned to cold, and that are not exposed to repeated thaws accompanied by rain, freezing rain, or sleet, can withstand very low temperatures, for the species is present in the vicinity of White River, Ont., which is one of the coldest places in Canada. Early snow cover and steady, continuing cold are ideal for overwintering larvae. Repeated rapid thawing and freezing under damp conditions are detrimental.

As long as the ideal conditions listed above persist, weather cannot be considered a limiting factor in the development of spruce budworm populations, and, in fact, should be considered a factor promoting rapid population growth. The ideal weather types occur, particularly in the Boreal forest, whenever a region is exposed to invasions of polar continental air. Modified

polar air masses, especially, would provide the particular seasonal requirements. Modified tropical maritime air, on the other hand, invading a region directly or aloft, would provide the adverse conditions noted. These air

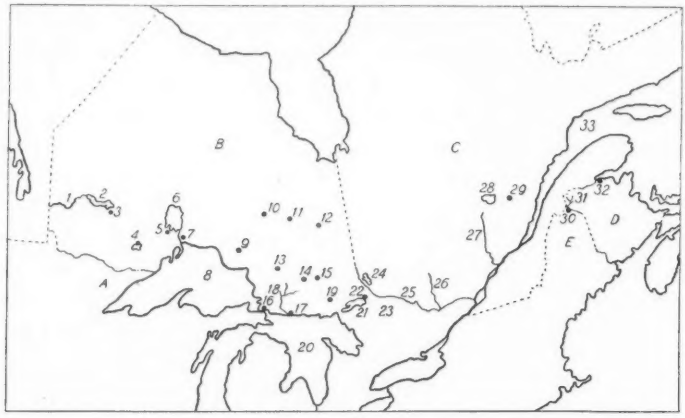

FIG. 2. *Map of the localities mentioned in the text. A—Northeastern Minnesota; B—Ontario; C—Quebec; D—New Brunswick; E—Maine; 1—English River; 2—Lac Seul; 3—Sioux Lookout; 4—Savanne; 5—Black Sturgeon Lake; 6—Lake Nipigon; 7—Cameron Falls; 8—Lake Superior; 9—White River; 10—Hearst; 11—Kapuskasing; 12—Cochrane; 13—Chapleau; 14—Biscotasing; 15—Ruel; 16—Sault Ste. Marie; 17—Blind River; 18—Mississagi River; 19—Sudbury; 20—Lake Huron; 21—Lake Nipissing; 22—Rutherglen; 23—Algonquin Park; 24—Lake Kipawa; 25—Ottawa River; 26—Gatineau River; 27—St. Maurice River; 28—Lake St. John; 29—Chicoutimi; 30—Edmundston; 31—Green River; 32—Dalhousie; 33—St. Lawrence River.*

masses occur in the broad region under consideration, and there is an indication that their frequency of occurrence varies not only seasonally but also annually. This is considered in detail in the following section.

Physical Indicators

SOLAR INFLUENCES

A number of authors (9, 11, 16, 21, 23, 29) have discussed relationships between sunspots and insects. If dates of spruce budworm outbreaks, irrespective of locality, are entered on a curve of annual sunspot numbers, no consistent pattern is apparent. If the infestations are grouped according to the regions in which they occurred, a rough pattern emerges. The New Brunswick outbreaks that have been dated with reasonable accuracy, namely, those about 1878 and 1913–14, occurred just prior to the years when the curves began to rise. Outbreaks in the central portion of Quebec (1910–11; 1942) occurred on the descending sides of cycles near the minima. Outbreaks near the Quebec–Ontario boundary (1909; 1939–40) also were on the descending sides of cycles, but occurred about two years past the peaks. Outbreaks in north central Ontario (e.g., 1935) were on the rising sides of cycles, whereas

those recorded in northwestern Ontario (1939–40) were much like those on the Quebec–Ontario boundary. These facts are of interest in that they provide a suggestion of future trends, but no close relationship between solar activity and population growth is implied, for reasons elaborated in the succeeding subsection. Attempts to establish direct relationships should be viewed with caution.

Climatic Indicators

Air Mass Movements

In attempting to bridge the gap between solar and purely climatic phenomena, it is helpful to consider movements of air masses before considering changes in temperature and precipitation. Precise data on movements of air masses of different properties are not readily available, but the *Monthly Weather Review* provides a series of monthly maps recording the movements of high and low pressure centers in North America. Kullmer (19) grouped some of these data and pointed out an apparent relationship between solar cycles and shifts in the latitude of the so-called storm track. To obtain data in workable form, he laid out a grid based on each five degrees of longitude and each two and one-half degrees of latitude, and entered the annual total of cyclonic centers (Lows) passing through each rectangle. Iso-lines were drawn to join points having equal numbers of storms, and the lines joining points with the greater numbers bounded the position of the storm track on an annual map.

Somewhat different information was required for this survey. It was of interest to determine the numbers of cyclonic centers that had passed through the rectangles covering the districts in which spruce budworm outbreaks were known to have occurred. Consequently, the required basic information was extracted from Kullmer's published annual maps (19, 20) and from additional maps in the *Monthly Weather Review*. Three-year running means were taken to smooth the curves. The smoothed curves in Fig. 3 show the fluctuations in the annual numbers of cyclones passing through zones in which outbreaks have occurred. Specific information is given in detail in the legend. The tendency for an outbreak to begin in any area during or at the end of a period of decreasing annual numbers of cyclones is clear.

Although the method illustrated in Fig. 3 has advantages, there is an objection to it on the grounds that too much concern with the frequency of storms in the area represented by one rectangle leads to neglect of the fact that centers passing through adjacent areas, particularly those to the north, must exert an appreciable influence upon the climate within the rectangle. This objection is based on an assumption of divergent trends in adjacent rectangles. Divergence sometimes does occur. Therefore, since data were available for most of the continent, regional maps were drawn to give more weight to surrounding territories. These maps are shown in Figs. 4 to 8. The methods employed require additional comment.

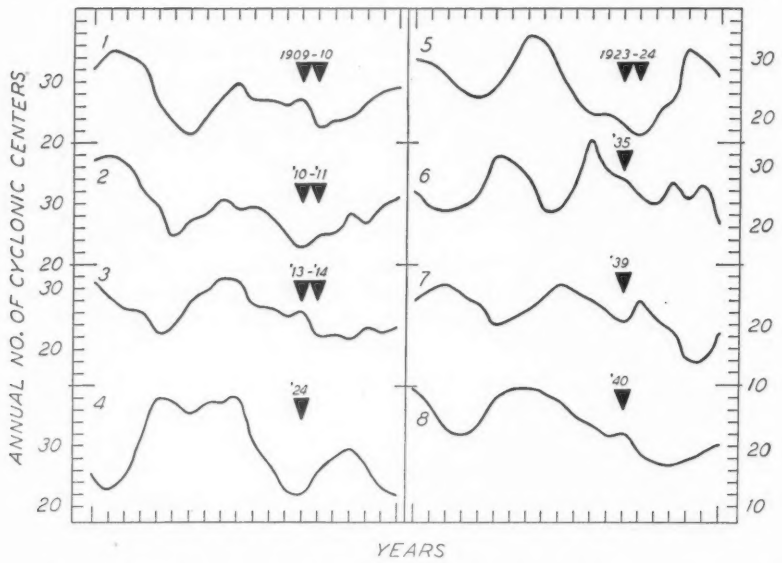

FIG. 3. *Dates of the beginnings of spruce budworm outbreaks in given areas plotted against the annual frequency of occurrence of cyclonic centers (centers of low pressure) in the areas. Each of curves 1–8 refers to a definite area during a definite period. 1: the upper Gatineau valley, P.Q.; 2: Lake St. John – St. Maurice region, P.Q.; 3: New Brunswick; 4: Savanne area, Ont.; 5: Biscotasing – Ruel area and east, Ont.; 6: Mississagi area, Ont; 7: Algonquin Park, Ont.; 8: Lake Nipigon, Ont.*

Annual numbers of cyclones were available for the period 1883–1947. Therefore, it was possible to compute a mean annual number for each rectangle of the grid. The means were entered in the rectangles, and iso-lines were drawn to give the average annual pattern. This is shown in Fig. 4.

Inspection of a group of curves similar to the fragments shown in Fig. 3 showed that, in the areas where outbreaks had occurred, the periods spanned by decreasing numbers of cyclones averaged approximately four years. Therefore, the remaining maps of the series were constructed on the basis of this number. The grid numbers for a four-year period preceding a given outbreak year were averaged, and their deviations from the long-term averages were obtained. These positive and negative deviations for each particular period were entered in the rectangles, and isonomals (lines of equal deviation) were drawn, with the results shown in Figs. 5 to 8.

Fig. 5 shows the conditions for 1906–1909, preceding the 1910–1911 Quebec outbreaks. Deficiencies are shown for the region containing the valleys of the Ottawa and Gatineau rivers, and thence northeastward along the height of land north of the St. Lawrence River. Negative deviations also appear in northern and northwestern Ontario. New Brunswick, on the contrary, is positive, as is the State of Maine.

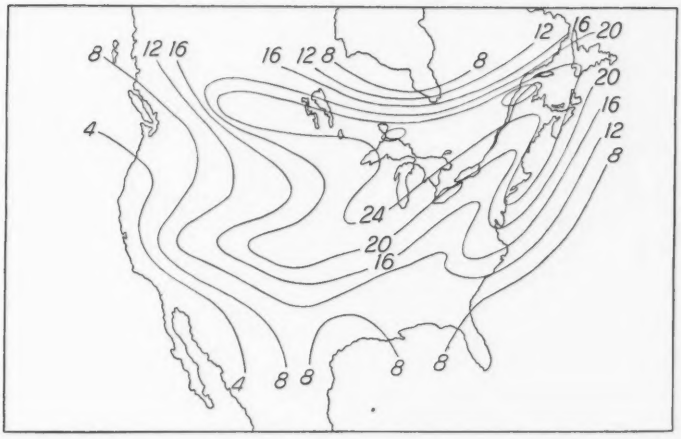

FIG. 4. *The average annual numbers of cyclonic centers over North America based on the period 1883–1947.*

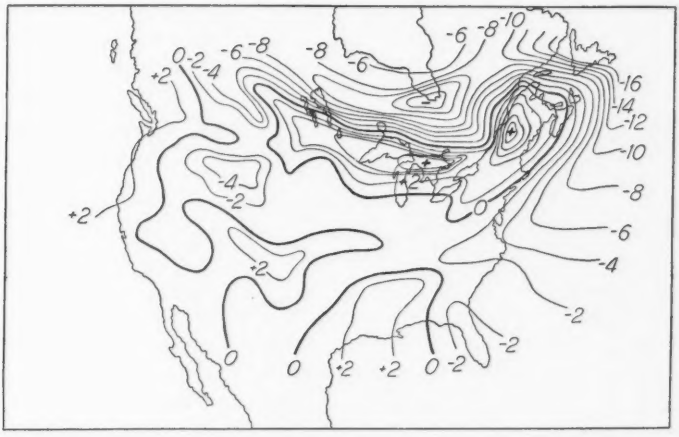

FIG. 5. *Deviations of the average annual numbers of cyclones for 1906–1909 from the long-term average, 1883–1947. Note the negative values over Quebec and the positive values over New Brunswick.*

Fig. 6 covers the period 1909–1912, preceding the 1913–1914 New Brunswick outbreaks. It shows negative deviations over most of the Province. The portion of Ontario north of Lake Superior is still negative, but, in addition, the northeastern third of the State of Minnesota is also negative.

Fig. 7 illustrates the conditions during 1931–1934, prior to the 1935 outbreak in the Mississagi area of Ontario. Negative deviations occur in the Mississagi area north of Lake Huron to the height of land, and thence eastward through the Lake Nipissing and Algonquin Park areas of Ontario into

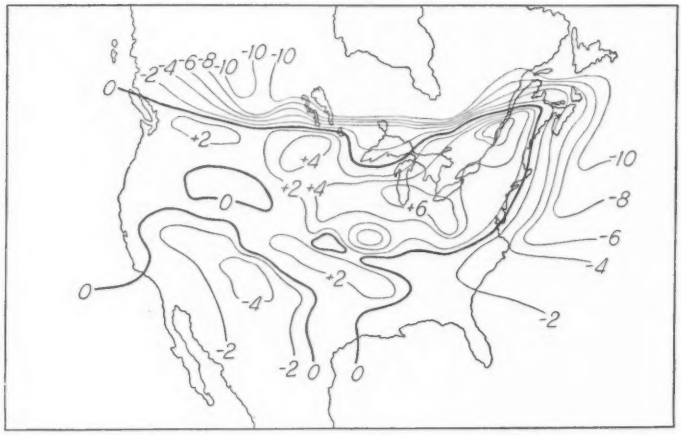

FIG. 6. *Deviations of the average annual numbers of cyclones for 1909-1912 from the long-term average, 1883–1947. Note the negative areas in northwestern Ontario, northeastern Minnesota, and New Brunswick, in contrast with the positive area over western Quebec (cf. Fig. 5).*

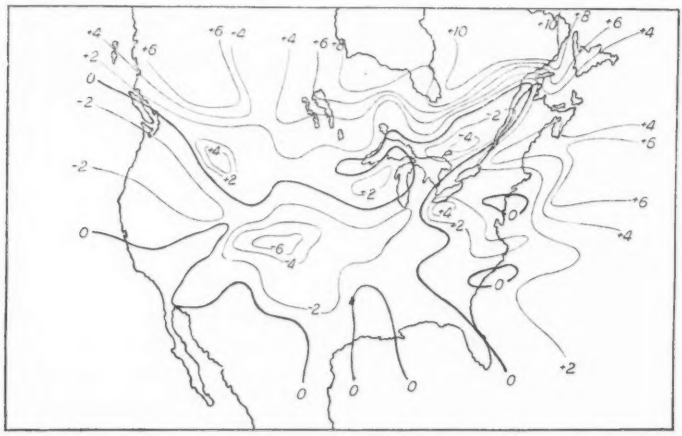

FIG. 7. *Deviations of the average annual numbers of cyclones for 1931–1934 from the long-term average, 1883–1947. Note the negative area north and east of Lake Huron and the positive area west of Lake Nipigon. In addition, note the negative area in southwestern United States, which compares with the area of the Dust Bowl.*

the Kipawa area of western Quebec, and eastward. An additional feature of some interest that is illustrated in this map is the negative zone in the Great Plains region which coincides remarkably well with the Dust Bowl zone of the 1930 decade (cf. 8).

Fig. 8 shows the deviations for 1936–1939, preceding the northern and northwestern Ontario outbreaks of 1940 *et seq.*, notably that which began on the western shore of Lake Nipigon. This area, which was positive in Fig. 7,

is negative in Fig. 8, as is the region westward into Manitoba. The negative area overlies points at which the Nipigon, Sioux Lookout (Hudson), and Lac Seul–English River outbreaks occurred during or shortly after 1940. To the

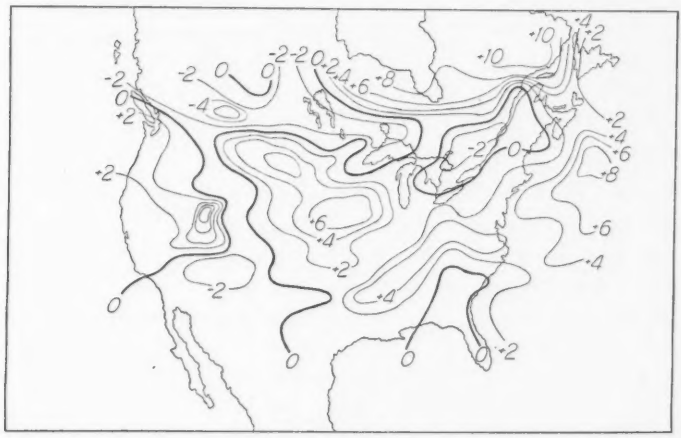

FIG. 8. *Deviations of the average annual numbers of cyclones for 1936–1939 from the long-term average, 1883–1947. Note the negative areas north and west of Lake Superior and east of Lake Huron, in contrast with the positive area north of Lake Huron (cf. Fig. 7).*

east, the Lake Nipissing – Algonquin – Lake Kipawa region containing the 1939 outbreaks of the spruce budworm is still negative, as are the contiguous portions of Quebec.

The foregoing maps demonstrate a marked tendency for negative deviations from average annual numbers of storms to occur in areas in which spruce budworm outbreaks are observed soon afterwards. A few discrepancies result from the method employed. For instance, the negative numbers in the Labrador region during 1906–1909 *et seq.* (Figs. 5 and 6) suggest a relationship that, on the basis of written accounts and of available meteorological data, did not occur. The isonomals in this region lack the weight of additional data for the region to the north during this early period, and should be regarded simply as end points for lines of uncertain direction. The positive zone covering Maine during the same period was not in keeping with the trend observed previous to spruce budworm outbreaks in New Brunswick, central and western Quebec, Ontario, and Minnesota. Studies of more detailed meteorological records suggest that this portion of the storm pattern was out of line with the fluctuations of at least the summer weather pattern. Nevertheless, although this indicates the method is not infallible, the association pointed out is too marked to be denied. In this connection, one might object that the deviations, taken as four-year averages, are so small that it is difficult to see what difference they might make. Further attention to the Dust Bowl zone outlined in Fig. 7 suggests that the method provides useful evidence of trends in climate.

The decreased number of cyclones that was generally associated with the periods immediately preceding outbreak dates should be considered with reference to the remarks concerning air mass types ideal for spruce budworm development, since cyclonic activity may be considered to be roughly related to the incidence of humid air masses.

In order to identify any apparent trends or fluctuations in climatic factors, it is necessary to examine the official meteorological records. The only long-term records of any practical application are those for temperature and precipitation.

Temperature

Official records are, unfortunately, of little practical value in the present problem. The spruce budworm, like all poikilotherms, is certainly influenced by temperature changes, but official records are of little value here. This objection goes deeper than the ecologists' usual objection to official data. It is not just a question of deviations of local air temperatures from station records; for the spruce budworm, because of its cryptic mode of life, is influenced much more by radiant heating and cooling than it is by air temperature (33). Therefore, it was found to be impossible to obtain any consistent relation between official air temperature changes and population changes.

Precipitation

As noted in the section on the physical requirements of the spruce budworm, there have frequently been indications that outbreaks of the insect or its effects on the tree were associated with periods of drought. Dry conditions may be taken as a rough index of available solar heating as well as of available moisture. A variation of polygonal graphing (18) was found to be the most satisfactory rapid method for comparing periods immediately preceding spruce budworm outbreaks either with monthly normals or with periods when no outbreaks occurred. The 12 months were plotted clockwise on polar coordinate paper, and the polygons, drawn to the same scale, were compared by transmitted light. The method is noted here because it is more graphic than most, but the polygons are not reproduced because they would take up too much space. In their place, a summarizing composite histogram of percentage deviations from the normals for several stations is given in Fig. 9. This illustrates the types of deviations encountered.

Each histogram in Fig. 9 is based on average monthly values for the four-year period immediately preceding the outbreak. This was done so that the figures would conform to the equivalent ones shown for the numbers of storms. Once again, the method tended to diminish some of the negative values, for no weighting against one large amount of rain in 24 hr. was done. Thus, one such rainstorm in a month had an inordinate effect. Nevertheless, the trends remain clear.

Diagram 1, for Chicoutimi, P.Q., shows a drought over the whole 12-month period for the interval 1906–1909. Diagram 2, for Dalhousie, N.B., shows spring and summer droughts, particularly, for the period 1909-1912. Diagram

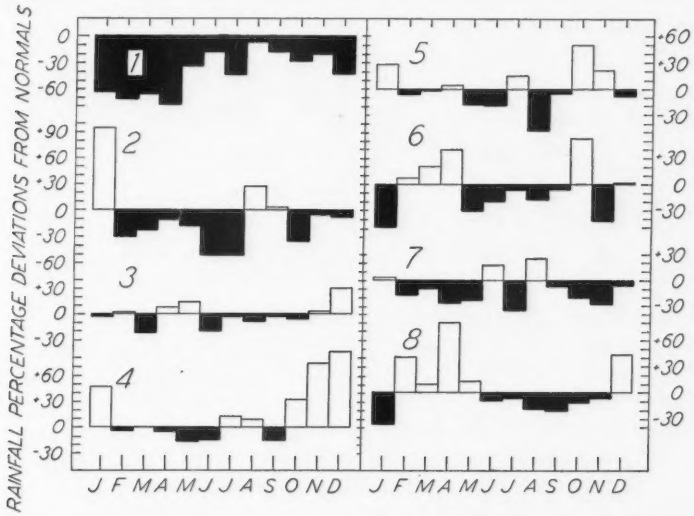

FIG. 9. *The percentage deviations from normal monthly precipitation of monthly values based on averages of four-year periods immediately preceding spruce budworm outbreaks. 1: Chicoutimi, P.Q., 1906-1909; 2: Dalhousie, N.B., 1909-1912; 3: Blind River, Ont., 1931-1934; 4: Biscotasing, Ont., 1932-1935; 5: Chapleau Ont., 1934-1937; 6: Rutherglen, Ont., 1935-1938; 7: Algonquin Park, Ont., 1935-1938; 8: Cameron Falls, Ont., 1936-1939.*

3, for Blind River, Ont., shows drought during the summer and autumn. Blind River was the closest station to the Mississagi outbreak that had a sufficiently long series of records to be of use during the period 1931–1934. Other, closer stations indicated greater decreases during the summers, but their records were fragmentary. Diagram 4, for Biscotasing, Ont., shows spring and summer droughts during the 1932–1935 period that preceded a wave of secondary outbreaks in that area of Ontario. During an earlier period, 1925–1931, the area about Biscotasing was just within the western fringe of an outbreak that began earlier, and it was only lightly infested. Diagram 5 shows conditions at Chapleau, Ont., during 1934–37, just prior to the beginning of a *light* infestation in that district. This area is of particular interest. During 1925–1928, when outbreaks occurred east of Chapleau but did not reach its immediate vicinity, the precipitation at Chapleau during both June and July was 54% above normal. In the Biscotasing–Ruel region to the east it was below normal during the same period.

Diagram 6 shows deviations at Rutherglen, Ont., during the preoutbreak period, 1935–1938, for the infestation that developed east and south of Lake Nipissing. A period of drought from spring to autumn is shown. Diagram 7

shows conditions in Algonquin Park, Ont., during the same period. Although June is shown to have above-normal precipitation, the distribution of the rainfall through the month suggests a diminished effect upon feeding, and this, coupled with the fact that available records indicate that the spruce budworm develops earlier in that region than to the west and north suggests that May and early June droughts were more important.

Diagram 8 shows conditions at Cameron Falls, Ont., which usually has approximately the same weather conditions as the area farther north (Chief Bay) where the Lake Nipigon infestation began. Even so, three widely spaced thunderstorms during June, 1938, each gave more than one inch of rain, and brought the influence of the Lake Superior shoreline weather belt to the station. This influenced the values inordinately so that the June negative deviation for 1936–1939 was diminished to a degree that is more apparent than real.

The detailed, yearly plots of individual months that are summarized in the four-year averages in Fig. 9 revealed a definite and consistent decrease in rainfall during the summer period, notably June and July, compared with either the normal values or the average values for months of periods lacking outbreaks. This association was indicated also by the more fragmentary records of other stations nearby. It was also found that the summer droughts were frequently accompanied by spring or autumn droughts, but seldom by both. Only rarely could a whole year be described as droughty.

Further points are reserved for the discussion, but a few additional findings may be noted at this point.* On the subject of precipitation, it is of interest to note that, in 1948 (10), it was reported that the spruce budworm was appearing in outbreak form north of Lake St. John, P.Q., and was threatening the coniferous stands of the North Shore region, where it had not appeared during the 1909 *et seq.* infestations. The few weather stations in the North Shore region of the St. Lawrence that were reporting during the first decade registered June precipitation frequently exceeding six inches during the pre-outbreak period. The normals for stations in this region range between about 3 and 3.6 in. On the other hand, in 1943–1947, June rainfall diminished from almost 4 in. to about 1.5 in., and July rainfall dropped from close to 5 in. to about 2 in. This contrast with the earlier period is interesting.

In the Green River area of New Brunswick, a study of the spruce budworm has been under way since 1944–1945 (4, 24). The first appreciable increase in population was observed during 1947, and this increase continued during 1948 but, during 1949, was not so great as had been expected. In 1937, a synchronized decline in precipitation at Edmundston, N.B., in June and July occurred for the first time since 1923, which was a few years after the outbreaks of 1913–1914 had run their courses. This synchronization occurred again in 1941 and 1946, so that its frequency of occurrence appears to be increasing. In addition, June rainfall diminished steadily from 6.17 in. in 1942 to 2.5 in. in 1946, but increased from 1947 to 1949. Extrapolation of rainfall curves suggests that June rainfall may begin to decline again in 1950 to a low in

1952 or 1953 and that July rainfall may begin to decline again about 1951. On this basis alone, no great increase in spruce budworm population should be expected until 1951; and, if no other factors, such as mass introductions from nearby populations, intervene, one may expect a moderate infestation, of the type that is usually considered to be a first-year outbreak, by 1952 or 1953. In addition, both storm numbers and sunspots should have declined by then. Since the blackheaded budworm, *Acleris variana* (Fern.), has been active in the same area on the same host, the situation may be unduly complicated.

With reference to storm numbers, the marked decline in northern Ontario noted in Figs. 5 and 6 was also reflected in the curve of annual storm numbers plotted for the rectangle west of Lake Nipigon. The trough is shown near the beginning of curve 4 in Fig. 3. Other things being equal, it would be expected that a spruce budworm outbreak might have begun somewhere in the region west of Lake Nipigon about 1912 or 1913. No observers were in this region at that time, and the fact that overmature trees occurred in the Nipigon area during the outbreak of 1940 *et seq.* suggested that there could not have been any severe outbreak near the district for many years. On the other hand, a broad area between Lake Nipigon and Sioux Lookout, Ont., is now covered by remnants of older forest and by regeneration stands from a fire in 1931 that was of sufficient proportions to suggest it was the aftermath of widespread spruce budworm damage. This was adopted as a working hypothesis in the winter of 1948–1949; and it was postulated that, if it were true, the focal area of the infestation, where most trees would be killed, was probably completely destroyed by the subsequent fire, but that peripheral portions of the infestation should still be evident in the ring patterns of trees in relict stands or on moister sites. The reasoning was that a spruce budworm infestation reaches its peripheral zone five to seven years after its initial appearance at the focus, and is then so subject to the ills of a mature population that it does not do sufficient damage to kill many trees. Because of diminished killing, less fire danger should exist, and trees in moister situations should survive. On the basis of the hypothesis, cores were taken from trees in the vicinity of Garden Lake, about 50 miles west of Lake Nipigon, in the summer of 1949. Marked and continued suppression of growth for a few years in a typical spruce budworm annual tree-ring pattern was found in some cores, beginning between 1916 and 1918. On the assumption that a primary focus became active in 1912 or 1913, the later dates agree well with the time lag postulated for the periphery of a mature infestation.

Finally, although this study has been confined to eastern North America, where the habits of the spruce budworm and conditions of forest and climate are better understood by the writers, it is worth noting an interesting relation between storm numbers and the spruce budworm outbreaks that are said to have begun in western Oregon in 1944 (2). The annual storm numbers for western Oregon are shown in Fig. 10. The relationship appears to be typical, even if an error of one year in dating is allowed. Local topographic influences on precipitation are of major importance in mountainous regions,

and it would be interesting to observe the relations of cloud types to radiation intensity and the amount and duration of precipitation on different types of slopes with reference to the distribution of the outbreaks.

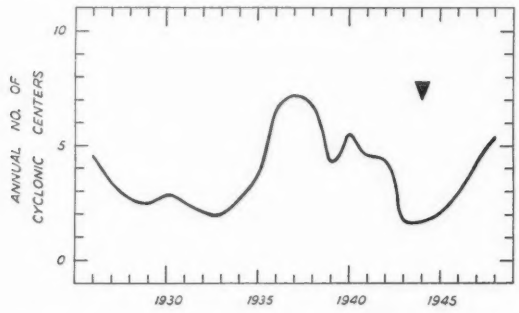

FIG. 10. *The assigned year of the beginning of spruce budworm outbreaks in western Oregon plotted against the annual frequency of occurrence of cyclonic centers in the region.*

Biological Indicators

RADIAL INCREMENT

Tree-ring analyses have always had an important part in the investigations of spruce budworm infestations because of the marked reaction of both balsam fir and white spruce to defoliation. It has been claimed (28) that discs taken near the base of a trunk will show an increased increment during the first season of obvious defoliation (i.e., the "outbreak" year of earlier authors), and a rapid decline through subsequent years of feeding, ending in either a slow recovery after the end of the outbreak, or cessation of growth and death. There is still room for scepticism regarding the value of the broad ring as a means of dating the first year of an outbreak. Nevertheless, if it is associated with subsequent decreased growth, and coupled with reduction in growth during the same year at the top of the tree, it is a reasonably accurate indicator of the abundance of the spruce budworm in an area in which it is suspected to have occurred. This growth pattern, however, is only an indicator of the appearance and course of the outbreak, not of the period of build-up preceding the outbreak, so that it is useless for predictive purposes.

Previously, the closest approach to a useful indicator of approaching outbreaks was the close association claimed by Bailey (3) for the frost rings that seemed to be formed during or immediately preceding the outbreak year. Frost damage severe enough to be reflected by the tree but still not harmful to young spruce budworm larvae is not quite in line with recent observations; but, even if this point is neglected, such a phenomenon would still be too close to the outbreak year to be of much predictive value. Moreover, its detection depends essentially upon laboratory techniques.

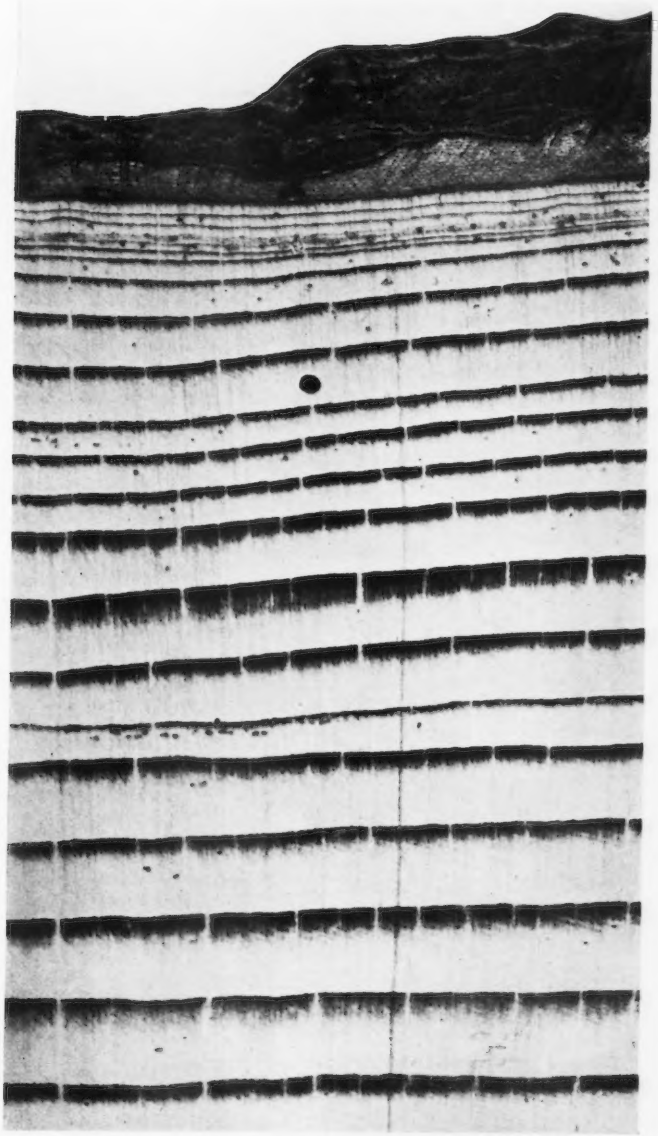

FIG. 11. *A portion of a disc taken near the base of the trunk of a dominant, 80-year white spruce from the vicinity of the Mississagi River, Ont. The dot marks the year 1935, which is also the year showing first great reduction in increment at the top of the trunk, and which is the year the spruce budworm outbreak began in the area. Effects of continued defoliation are apparent in the reduced growth near the periphery. Note the three years of slower growth prior to the ring marked with the dot.*

Annual rings, besides providing evidence of the course of an outbreak, also contain a convenient record of the earlier history of the tree. If the tree to be examined is not on a very moist site, there is often a suppression of growth for a few years preceding the outbreak year. This is shown in Fig. 11. This suppression is particularly marked in trees that show a later severe reaction to feeding. It cannot be confused with that existing prior to the initial release of the tree, for this occurs much earlier. Nor can it be confused with decadence, for it may be observed in trees vigorous enough to recover after attack. Besides the section shown in Fig. 11, examples of a similar three- or four-year suppression pattern prior to outbreaks may be found in illustrations published without comment on this point in earlier works (3, 38).

The Forest Tent Caterpillar

Examinations of Forest Insect Survey maps showed that outbreaks of the forest tent caterpillar, *Malacosoma disstria* Hbn., a feeder on deciduous trees, preceded outbreaks of the spruce budworm in several areas of Ontario and the contiguous area of Quebec. Although the first year of population increase of the tent caterpillar had no fixed relation, in time, to the first year of a spruce budworm outbreak, the year in which heavy feeding by the tent caterpillars was first observed occurred two to four years before the spruce budworm outbreak. This relationship is shown in Table I.

TABLE I

Observed intervals of time between the years in which forest tent caterpillar outbreaks reached the heavy feeding stage and the years in which spruce budworm outbreaks began in Ontario and the adjacent part of Quebec

Area	Beginning of heavy feeding by tent caterpillar	Spruce budworm outbreak year	Difference in years between outbreaks of spruce budworm and of tent caterpillar
Mississagi	1932	1935	+3
Sudbury	1935	1938	+3
Nipissing – Algonquin	1935–1936	1939	+3 to +4
Lake Kipawa	1937	1939	+2
Lake Nipigon	1938	1940	+2
Hearst – Cochrane – Kapuskasing	1941	1943–1944	+2 to +3

In the areas noted in Table I, the spruce budworm outbreaks were wellnigh superimposed upon those of the preceding outbreaks of tent caterpillars, or were offset slightly because of differences in forest composition. The relationships were particularly striking in the Algonquin Park district and along the Ottawa valley north of the Park to Lake Kipawa, where the boundary lines followed one another to a remarkable degree.

In addition to the areas listed in the table, older records show that a tent caterpillar outbreak began about 1910 in New Brunswick, and died out in 1914. Spruce budworm outbreaks began there in 1913 and 1914. The records available do not suggest any tent caterpillar infestations preceding the Quebec outbreaks in 1909, 1910, and 1911.

In Ontario, an extremely large outbreak of the tent caterpillar began in the northwestern region about 1933. It was centered west of Lac Seul, and appeared to reach its heavy feeding stage about 1936, when its boundaries also encompassed the area in the vicinity of Sioux Lookout. In July, 1945, active infestations of the spruce budworm were discovered near Lac Seul (7). These were supposed to have begun at some time between 1942 and 1944, but they were not dated accurately. Subsequent observations of host mortality indicate that the outbreaks may have started before 1942. In addition, the spruce budworm became active in the Sioux Lookout – Hudson area from about 1942 onward. The dating of the spruce budworm outbreaks is uncertain, but relationships in time and place are again suggested.

In addition, forest tent caterpillar infestations occurred in New Brunswick in the first half of the 1940 decade, and the peak was apparently reached in 1945 (26). Although the spruce budworm is not yet present in the Green River district in outbreak form, its first real increase in population was observed in 1947 (24). If one considers spruce budworm population increases instead of outbreaks, this would appear to be an additional example of the observed association.

Discussion

In the preceding sections, various physical and biological phenomena have been described that, in aggregate, proved to be consistent in their occurrence before known spruce budworm outbreaks. This discussion is concerned with drawing these phenomena together to show interlocking of pertinent events. First, attention will be given to the ordinary meteorological factors.

Official temperature records were of no value in the historical survey, so that discussion of temperature must be limited and precedence given to precipitation. Nevertheless, it should not be forgotten that the thermal effects, chiefly from radiant processes, are of basic importance in the life cycle of the spruce budworm.

The occurrence of droughts in the three- or four-year periods preceding outbreaks is well established. The occurrence of droughts in June and July has been especially noticeable in the preoutbreak periods; and this tendency often, but not always, carried over into the early years of infestation. There is no doubt that declining precipitation is closely associated with the beginning of population growth. It is also interesting that declining infestations are sometimes associated with increasing precipitation. The association between fluctuating precipitation and the outbreaks cannot be completely coincidental. Two types of relationships are implied by the available data: the relation of

the amount and duration of precipitation and sunlight to the physical requirements of the insect, and the relation of effective precipitation and light to the requirements of the host tree.

Citations have been given that outline the effects of atmospheric moisture upon the larvae of the spruce budworm during their feeding period. Feeding interrupted as little as possible by humid conditions should benefit survival, and possibly also fertility and fecundity. The observed occurrence of spring or autumn droughts may be related to decreased fluctuations in temperature (i.e., fewer thaws) noted as a desirable feature, since an increased number of storms implies an increased number of invasions by warm air masses that would be attended by violent temperature fluctuations as well as by increased precipitation. Although temperature and precipitation effects may occur in any month of the year, the amount or the duration of precipitation in June and July appear adequate as indicators when considered year by year.

Concerning the host tree, although effective moisture supply is controlled to an important extent by precipitation over the year, the period of June and July is an important part of the growing season. There can be no argument about the need for moisture, but it is not clear whether the effects of lack of moisture on the tree are related to spruce budworm population growth. Further research on this aspect of the problem is needed. Several possibilities may be considered: (*a*) The association may be wholly coincidental. (*b*) The resistance of the tree may be lowered, although it is difficult to see how this could affect population growth unless a change took place in the chemical composition of foliage of trees subject to drought, providing a better food for the spruce budworm than foliage of more vigorous, well watered trees. (This field of research is, as yet, relatively untouched.) (*c*) Production of staminate flowers (5) may be increased under adverse conditions, conceivably favoring spruce budworm larvae in a small population as it appears to do during outbreaks (6). Research now in progress in Ontario should provide answers to some of the questions.

Precipitation warrants consideration as a practical indicator. When the more complex physical phenomena are considered, direct application of sunspot data is apparently a procedure that has no safe basis at present, even if data were readily obtainable whenever they were required. The indicated associations noted in the earlier section should be kept in mind, but it is doubtful whether any very direct relationship will be found. Spruce budworm outbreaks had to be grouped for restricted areas before they could be placed on the curves of sunspots in approximately constant positions. This suggests localized control, such as that associated with fluctuating annual numbers of low pressure centers. The more or less regular fluctuations of the annual numbers in given areas illustrated in Fig. 3 were not always synchronized. The fluctuations occurred because of shifts in the position of the storm track. The apparent lack of synchronization, particularly in some adjacent areas of Ontario, appears to be a result of the Y-shaped structure of the track.

The tendency for outbreaks of the spruce budworm to begin during a period of decreasing annual numbers of cyclones was shown in Fig. 3. There are recurring decreases in the annual numbers within short periods in any area, and, superficially, there should be no reason why outbreaks occur in one trough and not in the next. The chief reason why this repetition cannot occur is that trees in the area must be relatively mature, for no outbreaks have yet been observed to *begin* in immature stands of balsam or spruce. Hence if destructive outbreaks have occurred in an area, time is required for the development of new, susceptible stands. The important point is that, when outbreaks occur, it is during periods of decreasing or minimal storm numbers. Therefore, although tree maturity is the preparatory cause of outbreaks mentioned by Graham and Orr (15), climatic factors form the immediate cause that they postulated as a necessary addition to the causal chain.

Fig. 3 indicates also that the more severe known outbreaks continued to increase in intensity while the eventual increase in storm numbers was gradual, whereas less severe outbreaks occurred at times when the curve of storm numbers rose quickly again (e.g., areas 4 and 5, Fig. 3). This point has interesting possibilities for those interested in factors associated with the termination of outbreaks. The 1923–1924 outbreak that eventually covered the Sudbury–Ruel–Biscotasing region of central Ontario has seldom been considered a minor outbreak. Nevertheless, it left sufficient host stands for development of additional outbreaks throughout the area some 12 years later, at a time, incidentally, of another decrease in storm numbers.

Fluctuations of populations of the forest tent caterpillar in an area are valuable in indicating possible spruce budworm outbreaks, even when the two species do not occur in the same stands. In Ontario, the years in which primary outbreaks of this tent caterpillar begin in different areas seem to be associated with greater numbers of storms, in contrast with the relationship observed between the spruce budworm and storm numbers. The implication for both species is that conditions favoring population growth rapid enough to produce outbreaks occur in the few years prior to the outbreak dates. For the spruce budworm, this means that its population level in suitable forests begins to rise as storms decrease in frequency; that is, the population rise begins during a period when the tent caterpillar may be present in active outbreak. This suggests that there may sometimes be more than a mere coincidence in time between the two species in forests where they are closely associated. This leads to several points outlined below. They form a subject that is being actively investigated at present, the results of which will be published at a later date (12).

It is generally considered that the forest tent caterpillar does little harm to *Populus* spp. and its other hosts. This is not invariably true. Overmature poplars become decadent, but about 20 years is required to eliminate the original stand if the trees are not attacked by tent caterpillars. On the other hand, if such trees are severely defoliated by tent caterpillars for two or three years, the period of decadence and elimination may be shortened to five to

seven years. A great deal of the present forest of north central and northwestern Ontario consists of poplar or birch overstory with an understory of balsam fir. Stages of succession from pure poplar or birch overstory to nearly pure conifer may be observed over short distances. Anything that hastens the succession so that conifers become dominant tends to increase the susceptibility of the stand to spruce budworm attack. If this succession occurs during the climatic fluctuation in advance of the one associated with a spruce budworm outbreak, the susceptibility of the area is greatly increased. If it occurs during the period of drought that frequently carries over into the early outbreak period, additional areas are opened up that would be relatively untouched otherwise, and the outbreak becomes more severe.

Previous reference was made to an early spruce budworm outbreak, about 1913–1918, that was located, through storm-track analysis, west of Lake Nipigon. It was mentioned that at first it was thought no outbreak could have occurred because dense stands of overmature hosts of the spruce budworm were present on the shores of Lake Nipigon in 1940. These stands presumably would have been attacked during any outbreak in the 1910–1920 decade. When the presence of the outbreak was established, closer attention to the western shore of Lake Nipigon showed remnants of poplar stands over 100 years old, the remaining trees of which were attacked by the forest tent caterpillar in 1938 and 1939. The poplar must have been dominant in the 1910 decade, and the reason why no serious spruce budworm problem arose in this area then, while it arose farther west, is evident. In districts where the two species of insects occur in very different forest types, their observed succession in time is undoubtedly due to their different climatic requirements; but, where the forest type is like that described above, it is reasonable to conclude that the forest tent caterpillar is a potent ally of the spruce budworm.

The points treated above lead to some pure speculation that may appear to be of doubtful value, but that should be kept in mind during future observations. The observed grades of susceptibility, to the spruce budworm, among stands with varying content of dominant poplar during the preoutbreak period, and the effects of exposure of host trees on population growth under suitable physical conditions, suggest that an effective exposure may occur if complete defoliation of poplar were to occur at the same time that physical conditions were changing in favor of the spruce budworm. This need not involve elimination of the poplar trees, but only temporary elimination of their foliage. It has been noted that there is some overlap in time between the period of heavy defoliation by tent caterpillars and the preoutbreak period of rapid population growth of the spruce budworm. The seasonal feeding periods of the two species also overlap to a marked extent. Removal of poplar leaves would temporarily expose overtopped large conifers in a manner that should be comparable to that produced by slower removal of whole poplar trees, and physical conditions for larvae on the conifers should more closely approximate conditions on dominant trees during the period the overtopping foliage is absent. Such conditions may not occur often; otherwise stands

under poplar should be attacked more frequently. However, we have dealt chiefly with past outbreaks where stand histories have often been imperfectly known. Future observations should provide more detailed information.

Some comments on current concepts of spruce budworm population dynamics may not be misplaced. These comments lead directly into the sphere of actual outbreaks, which, strictly speaking, is not within the province of this paper. Some of the comments have been made before (14), but the need for repetition is still apparent.

First, it is often implied that outbreaks starting in central Ontario spread eastward until they pass through Quebec and reach the Maritime Provinces. There can be no objection to statements about spread along the advancing margin of a given infestation as long as the distances are kept within reasonable limits, for it has been demonstrated that several stages of the insect are susceptible to aerial dispersal under well defined meteorological conditions (17). On the other hand, the association of specific patterns of precipitation and storms with outbreaks in definite areas suggests that it would be wiser to restrict statements about spread to the limits of these areas. There is an endemic population over the whole subcontinental region of suitable forest. Therefore, it is more reasonable to postulate the development of different foci in definite areas when, and only when, conditions permit, than to speak in terms of an infestation that advances inexorably across a third of the continent.

Second, until the Green River Project was begun, entomologists have been able to study the spruce budworm only during outbreaks, and this has colored their thinking about the complex of factors involved. Solomon (27) has recently set forth an exposition on control of populations that should make it clear that it is unwise to argue too vehemently for particular factors of a complex. Nevertheless, the phenomena set forth in this paper have not been seriously considered before.

Much of the philosophy concerning the natural control of insect populations that has developed on this continent has drawn upon experience with major pest species that have been introduced from other continents. The spruce budworm is a native insect. There has been so much preoccupation with the reactions of forests to human influences that it is easy to overlook the fact that some of the severest known outbreaks of the spruce budworm occurred in virgin forests, and there is reason to postulate a recurrence of outbreak conditions in the past similar to those that have been observed in recent times. Pollen analyses have shown long-term postglacial changes in forest types; but if divisions much finer than one foot were generally adopted for analyses of North American pollen cores, there is reason to suppose that shorter fluctuations, still of the order of a few hundred years, would be revealed as they have been in Europe (cf. 1, 25). Therefore, conditions of forest and climate very similar to those now existing in the Boreal region might have recurred several times during the past few thousand years, although the storm track might have been at different mean latitudes during different periods.

A native insect that has this indicated background and that exhibits violent fluctuations in population density cannot be governed by parasites and diseases during its periods of minimal or initially increasing density so much as by a combination of forest type and climate. The current survey has indicated that endemic populations in the susceptible foci begin to grow to outbreak proportions when the climatic control is relaxed. There has been no indication of control or release of populations by parasitic or pathogenic agents during the long period of minimal density or during the initial population growth in the foci.

During the first portion of the outbreak period, biological control agents increase in numbers; but observations in the Lake Nipigon infestation indicate that the spruce budworm population begins to experience other troubles, some of which, like starvation, are self-inflicted, shortly before the biological agents assume an important role. The relationships are complex, but there are now field indications that starvation and specific reactions to meteorological factors that drive large numbers of larvae from the trees prior to pupation (30) may decrease the spruce budworm population just enough to make it extremely vulnerable to the rapidly increasing populations of biological agents (B. M. McGugan, personal communication).

Recognition of the master factors in the preoutbreak complex suggests that programs for the chemical and biological control of the insect should be weighed with reference to these factors. During the period of initial increase of the population, much serious thought should be given to such proposed attempts at control before they are embarked upon. Later in an outbreak, judicious selection of areas for spraying or release of biological agents might have beneficial results.

Conclusions

1. Ideal physical conditions for spruce budworm development are sunlight and lack of rainfall.

2. Dry conditions that also provide more sunlight in spring and summer and continued cold in winter are associated more with polar continental air masses than with maritime air masses.

3. An historical survey of some known outbreaks in northeastern North America showed recurrence of several physical and biological phenomena in the three- or four-year periods preceding assigned outbreak dates.

4. Annual numbers of cyclonic centers passing through restricted areas may be taken as indices of air mass movements. The numbers decreased before outbreak dates, so that outbreaks occurred during periods of decreasing or minimal numbers.

5. Official precipitation records are rough indices both of moisture and of available sunlight. Precipitation fell below normal during the preoutbreak periods. Droughts in June and July were most common, but sometimes spring or autumn droughts also were associated with these summer dry periods.

6. Radial increments in basal sections of host trees from moderately dry sites decreased during the preoutbreak periods, presumably in response to decreased precipitation.

7. In areas of Ontario where forests contained much poplar as well as balsam fir, heavy feeding by the forest tent caterpillar preceded severe spruce budworm outbreaks, and there were some indications of a similar association in western Quebec and in New Brunswick.

8. These phenomena recurred often enough that, in aggregate, they are worth testing as indicators of future outbreaks.

9. Examination of available evidence indicates that forest composition is a preparatory cause of outbreaks but that relaxation of climatic control is the immediate cause of rapid population growth to the outbreak stage in susceptible foci.

10. Recognition of the existence of an endemic population throughout northeastern North America, which reacts to relaxation of climatic control in suitable foci, is preferable to assumption of spread of an infestation over distances up to 1000 miles.

Acknowledgments

It is a pleasure to acknowledge the helpful criticism of M. L. Prebble, Officer-in-Charge of the Forest Insect Laboratory, Sault Ste. Marie, Ont. In addition, the writers wish to thank W. R. Henson, J. R. Blais, D. A. Fraser, and B. M. McGugan, of that laboratory, for useful suggestions and, in some instances, for permitting inspection of basic unpublished data.

References

1. AHLMANN, H. W. The present climatic fluctuation. Geograph. J. 112 : 165-195. 1949.
2. ANONYMOUS. Spruce budworm control plan for 1950 in Oregon and Washington. Portland, Oregon. 1949.
3. BAILEY, I. W. The "spruce budworm" biocoenose. I. Frost rings as indicators of the chronology of specific biological events. Botan. Gaz. 80 : 93-101. 1925.
4. BALCH, R. E. Spruce budworm. *In* Forest Insect Invest. Bi-monthly Progress Rept. 1 (5), pp. 1–2. Can. Dept. Agr. 1945.
5. BESS, H. A. Staminate flowers and spruce budworm abundance. *In* Forest Insect Invest. Bi-monthly Progress Rept. 2 (2), pp. 3–4. Can. Dept. Agr. 1946.
6. BLAIS, J. R. The spruce budworm in relation to flowering condition of the host tree (field investigations). *In* Forest Insect Invest. Bi-monthly Progress Rept. 4 (5), p. 1. Can. Dept. Agr. 1948.
7. BRADLEY, G. A. Northern Ontario: Species causing serious injury at the present time. *In* Annual Report of the Forest Insect Survey, 1945, p. 36. Can. Dept. Agr., Ottawa. 1946.
8. CHOUN, H. F. Duststorms in the southwestern plains area. U.S. Weather Bur. Monthly Weather Rev. 64 : 195-199. 1936.
9. CRIDDLE, N. The correlation of sunspot periodicity with grasshopper fluctuations in Manitoba. Can. Field-Naturalist, 46 : 195-198. 1932.
10. DAVIAULT, L. Present status of the spruce budworm outbreak. *In* Forest Insect Invest. Bi-monthly Progress Rept. 4 (4), p. 1. Can. Dept. Agr. 1948.
11. EIDMAN, H. Zur Kenntnis der Periodizität der Insektenepidemien. Z. angew. Entomol. 18 : 537-567. 1931.
12. FETTES, J. J. Interrelationships of the spruce budworm, the forest tent caterpillar and their host trees in northern Ontario. Unpublished Ms.

13. FRANZ, J. Der Tannentriebwickler *Cacoecia murinana* Hb. Beitrage zur Bionomie und Ökologie. Z. angew. Entomol. 27 : 345-407; 585-620. 1940.

14. GRAHAM, S. A. Forest insect populations. Ecol. Monographs, 9 : 301-310. 1939.

15. GRAHAM, S. A. and ORR, L. W. The spruce budworm in Minnesota. Minn. Agr. Expt. Sta. Tech. Bull. 142. 1940.

16. HEADLEE, T. J. Cycles of abundance of the eastern tent caterpillar (*Malacosoma americana* Fabr.). New Jersey Expt. Sta. Bull. 579. 1934.

17. HENSON, W. R. The means of dispersal of the spruce budworm, *Choristoneura fumiferana* (Clem.). Ph. D. Thesis. Yale University. 1950.

18. HUTCHINSON, A. H. Polygonal graphing of ecological data. Ecology, 21 : 475-487. 1940.

19. KULLMER, C. J. The latitude shift of the storm track in the 11-year solar period. Smithsonian Inst. Pubs. Misc. Collections, 89, No. 2. 1933.

20. KULLMER, C. J. A remarkable reversal in the distribution of storm frequency in the United States in Double Hale Solar Cycles, of interest in long-range forecasting. Smithsonian Inst. Pubs. Misc. Collections, 103, No. 10. 1943.

21. DE LURY, R. E. Sunspot influences. J. Roy. Astron. Soc. Can. 32 : 1-50. 1938.

22. MACALONEY, H. J. Relation of root condition, weather and insects to the management of jack pine. J. Forestry, 42 : 124-129. 1944.

23. MACLAGAN, D. S. Sunspots and insect outbreaks: an epidemiological study. Proc. Univ. Durham Phil. Soc. 10 : 173-199. 1940.

24. MORRIS, R. F. Green River Project—summary of entomological investigations in 1947. *In* Forest Insect Invest. Bi-monthly Progress Rept. 4 (1), p. 1. Can. Dept. Agr. 1948.

25. POST, L. VON. The prospect for pollen analysis in the study of the earth's climatic history. New Phytologist, 45 : 193-217. 1946.

26. REEKS, W. A., FORBES, R. S., and CUMING, F. G. Maritime Provinces and Newfoundland: Species causing injury at the present time. *In* Annual report of the Forest Insect Survey, 1946, p. 9. Can. Dept. Agr., Ottawa. 1947.

27. SOLOMON, M. E. The natural control of animal populations. J. Animal Ecol. 18 : 1-35. 1949.

28. SWAINE, J. M., CRAIGHEAD, F. C., and BAILEY, I. W. Studies on the spruce budworm *Cacoecia fumiferana* Clem. Can. Dept. Agr., Tech. Bull. 37. 1924.

29. UVAROV, B. P. Insects and climate. Trans. Entomol. Soc. London, 79 : 1-247. 1931.

30. WELLINGTON, W. G. The light reactions of the spruce budworm, *Choristoneura fumiferana* Clemens (Lepidoptera: Tortricidae). Can. Entomologist, 80 : 56-82A. 1948.

31. WELLINGTON, W. G. The effects of temperature and moisture upon the behaviour of the spruce budworm, *Choristoneura fumiferana* Clemens (Lepidoptera: Tortricidae). I. The relative importance of graded temperatures and rates of evaporation in producing aggregations of larvae. Sci. Agr. 29 : 201-215. 1949.

32. WELLINGTON, W. G. The effects of temperature and moisture upon the behaviour of the spruce budworm, *Choristoneura fumiferana* Clemens (Lepidoptera: Tortricidae). II. The responses of larvae to gradients of evaporation. Sci. Agr. 29 : 216-229. 1949.

33. WELLINGTON, W. G. Effects of radiation on the temperatures of insectan habitats. Sci. Agr. 30 : 209-234. 1950.

34. WELLINGTON, W. G. Variations in the silk-spinning and locomotor activities of larvae of the spruce budworm, *Choristoneura fumiferana* (Clem.), at different rates of evaporation. Trans. Roy. Soc. Can., Sect. V. To be published.

35. WELLINGTON, W. G. and HENSON, W. R. Notes on the effects of physical factors on the spruce budworm, *Choristoneura fumiferana* (Clem.). Can. Entomologist, 79 : 168-170; 195. 1947.

36. WOLFE, J. N. The use of Weather Bureau data in ecological studies. Ohio J. Sci. 45 : 1-12. 1945.

CANADIAN JOURNAL OF RESEARCH

Notes on the Preparation of Copy

GENERAL:—Manuscripts should be typewritten, double spaced, and the **original and one extra copy** submitted. Style, arrangement, spelling, and abbreviations should conform to the usage of this Journal. Names of all simple compounds, rather than their formulae, should be used in the text. Greek letters or unusual signs should be written plainly or explained by marginal notes. Superscripts and subscripts must be legible and carefully placed. Manuscripts should be carefully checked before being submitted, to reduce the need for changes after the type has been set. If authors require changes to be made after the type is set, they will be charged for changes that are considered to be excessive. **All pages, whether text, figures, or tables, should be numbered.**

ABSTRACT:—**An abstract of not more than about 200 words, indicating the scope of the work and the principal findings, is required.**

ILLUSTRATIONS:

(i) *Line Drawings:*—All lines should be of sufficient thickness to reproduce well. Drawings should be carefully made with India ink on white drawing paper, blue tracing linen, or co-ordinate paper **ruled in blue only**; any co-ordinate lines that are to appear in the reproduction should be ruled in black ink. Paper ruled in **green, yellow, or red should not be used** unless it is desired to have all the co-ordinate lines show. Lettering and numerals should be neatly done in India ink preferably with a stencil (**do not use typewriting**) and be of such size that they will be legible and not less than one millimetre in height when reproduced in a cut three inches wide. All experimental points should be carefully drawn with instruments. Illustrations need not be more than two or three times the size of the desired reproduction, but the ratio of height to width should conform with that of the type page. **The original drawings and one set of small but clear photographic copies are to be submitted.**

(ii) *Photographs:*—Prints should be made on glossy paper, with strong contrasts; they should be trimmed to remove all extraneous material so that essential features only are shown. Photographs should be submitted **in duplicate;** if they are to be reproduced in groups, one set should be so arranged and mounted on cardboard with rubber cement; the duplicate set should be unmounted.

(iii) *General:*—**The author's name, title of paper, and figure number should be written in the lower left hand corner (outside the illustration proper) of the sheets on which the illustrations appear.** Captions should not be written on the illustrations, but typed on a separate page of the manuscript. All figures (including each figure of the plates) should be numbered consecutively from 1 up (arabic numerals). **Each figure should be referred to in the text.** If authors desire to alter a cut, they will be charged for the new cut.

TABLES:—Titles should be given for all tables, which should be numbered in Roman numerals. Column heads should be brief and textual matter in tables confined to a minimum. **Each table should be referred to in the text.**

REFERENCES:—**These should be listed alphabetically by authors' names, numbered in that order, and placed at the end of the paper.** The form of literature citation should be that used in the respective sections of this Journal. **Titles of papers should not be given in references listed in Sections A, B, E, and F, but must be given in references listed in Sections C and D.** The first page only of the references cited in papers appearing in Sections A, B, and E should be given. **All citations should be checked with the original articles.** Each citation should be referred to in the text by means of the key number; in Sections C and D the author's name and the date of publication may be included with the key number if desired.

Reprints

Fifty reprints of each paper without covers are supplied free. Additional reprints, if required, will be supplied according to a prescribed schedule of charges. On request, covers can be furnished at cost.